

Extracts and Enzymic Hydrolysates from Fish Liver and Mammalian Liver¹

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ABSTRACT

Extracts and enzymic hydrolysates were prepared from cod, haddock, salmon, whale, seal, beef and pork livers. Extraction was carried out with water at pH 5; enzymic hydrolysis was effected by papain at pH 5.5 and at 65°C. followed by pancreatin at pH 7.5 and at 50°C. The proper digestion times were established. Extracts, as well as hydrolysates, were concentrated by distillation *in vacuo* to the consistency of syrup and then dried at a low temperature *in vacuo*. The preparations were analysed for a large number of inorganic and organic constituents. Comparisons of the results for preparations from fish livers with corresponding products from mammalian livers lead to the conclusion that fish livers are useful raw materials for the production of extracts and enzymic hydrolysates for use in foods or in medicinal preparations.

INTRODUCTION

SINCE Minot and Murphy (1926) published their first achievements of the administration of liver to patients suffering from pernicious anaemia, the nutritional and curative properties of liver have been subjected to extensive research, the active principle has been found and isolated, and its chemical and physical properties have been studied.

Mammalian liver, particularly beef liver, has not only been of importance in liver therapy, but was also one of the cheapest sources of good proteins for those peoples who could not afford to buy more expensive cuts of meat. During the past ten years, however, the cost of mammalian liver has risen steadily, with the result that those who need it most can least afford it.

Potentially, a large amount of fish liver is available which might be used to replace mammalian liver in the enrichment of the human diet and in the preparation of concentrates for medicinal use. Official statistics show that the total landings of cod, haddock, pollock and salmon for 1954 in Canada amounted to 1,009,000,000 pounds. Figures for whale and seal are not available, but the amount is considerable. If the livers from this quantity of marine mammals could be converted into a stable, palatable and salable product, a new source of good proteins and vitamins would have been found which could help alleviate the world's need for these nutrients.

Fish livers have been used as food only to a limited extent. They are generally high in oil, and the macerated tissue left after the removal of the greater part of the oil is not of an appearance acceptable to potential consumers. The nutritive properties have not been generally known.

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Researches, the results of which are reported here, were undertaken to transform these liver residues into a palatable, acceptable form that might be ingested alone, or incorporated with other foods into a diet, and to determine quantitatively some of the constituents that make the material nutritionally important. The most promising starting material for commercial utilization, particularly of fat livers, such as those of the cod family, appears to be the liver residue obtained by the method of Vandenheuvel (1952). This residue could be worked up directly from the centrifuge, or as a dry, quite stable material that contains the nutrient properties of the non-oily fraction of the fresh liver.

DEFINITIONS

Extracts are defined as the solutions obtained by extraction with water, with or without the presence of ethanol, at a certain pH and temperature. These solutions are either concentrated to a consistency of syrup or dried completely. Extracts contain all, or almost all, of the constituents of the raw material, which are soluble in the extractant used.

Enzymic hydrolysates are obtained from liver or liver residue after treatment with one or more enzymes.

RAW MATERIALS

1. Fresh whole livers of cod, haddock, or pollock.
2. Liver residue. Fresh livers were rinsed with water, minced and, after addition of 0.04 per cent sodium bisulphite (NaHSO_3) (Fricke *et al.*, 1950; Frost *et al.*, 1950; Guttman and Vandenheuvel, 1952), autoclaved for 15–20 minutes at 110–115°C. After cooling to 70°C., the mixture was centrifuged and the oil drained off. The remainder was mixed thoroughly.
3. Dried, defatted residue. Fresh liver residue, dried *in vacuo* at 50–55°C., ground to pass a 20-mesh sieve, and extracted in a Soxhlet apparatus with a 1, 2, dichlorethane (ethylene dichloride). The last traces of solvent were removed *in vacuo*.

PREPARATION OF EXTRACTS

To wet material, either whole livers or undried residue, twice the volume of water was added. The mixture was minced for two minutes in a Waring blender, brought to pH 5 with hydrochloric acid, and kept at 80–85°C. for 30 minutes, while stirring. It was then centrifuged to remove solids, and to the supernatant liquid, water was added to the original volume. This first extract was used in the extraction of a second batch of raw material: Figure 1 gives the complete procedure. The combined extracts were filtered, and the filtrate was evaporated *in vacuo* at 70°C. to one-third of the original volume. One-half of this concentrate was then further evaporated to dryness at 50°C. The other half was added to an equal volume of 95 per cent (v/v) ethanol, kept cool overnight and centrifuged. The precipitate was washed twice with small amounts of 50 per cent (v/v) ethanol and the combined supernates and washings were concentrated and dried *in vacuo*.

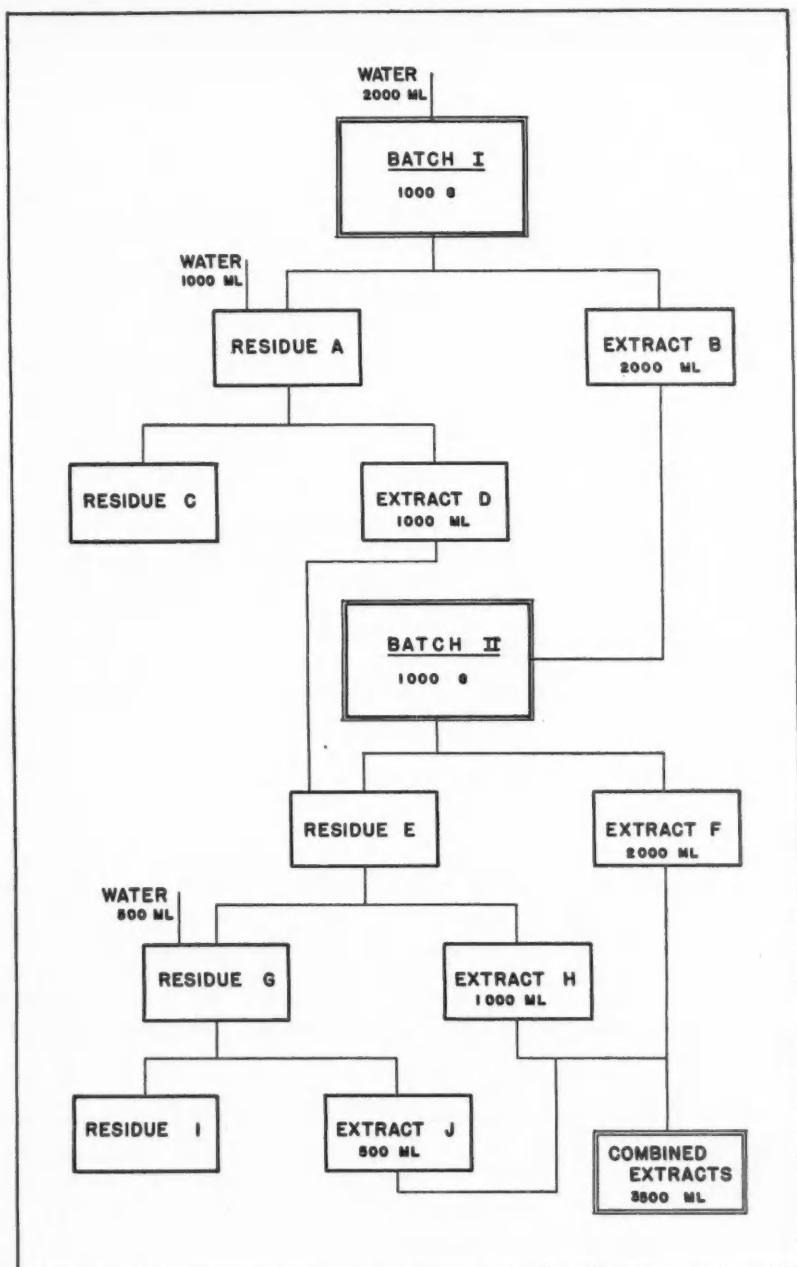


FIGURE 1. Extraction procedure.

The dry products were stored in sealed, amber glass containers.

Extracts from dried, defatted residue were prepared in the same manner, except that the ratio of water to material was 6 for the first extraction and 3 for the second.

PREPARATION OF ENZYMIC HYDROLYSATES

Hydrolysates were prepared from whole minced liver, dried liver defatted with dichlorethane, and dried and defatted liver residue.

Rinsed whole livers were minced with an equal weight of water and brought to pH 5.5 with hydrochloric acid. The mixture was warmed to 65°C. and papain³ (1 per cent of the dry weight of fat-free livers), dissolved in water, was added. After digestion for 6 hours with continuous stirring, the oil was siphoned off and the aqueous layer centrifuged. The solids were washed twice with water, and the combined liquids, brought to pH 6, heated to boiling, and then filtered and concentrated *in vacuo*, at 50°C., to one-third of the original volume. The remaining fat was removed by extraction with dichlorethane; the last traces of solvent were removed by treatment *in vacuo* at 50°C.

Dried, defatted liver, or dried, defatted residue was suspended in six times the weight of water. The mixture was brought to pH 5.5 with hydrochloric acid, and digested at 65–68°C. with papain (1 per cent of the weight of the material) for six hours, under continuous stirring. During this digestion, water was added to make up for evaporation losses. The solids, obtained by centrifuging, were suspended in half the initial amount of water, warmed to 50°C., and digested for 6 hours at pH 7.5 with pancreatin (U.S.P., 0.5 per cent of the weight of the original sample). The pancreatin digest was adjusted to pH 6, heated to boiling and, after cooling, filtered. The filtrates of both enzyme treatments were combined, concentrated, and dried *in vacuo*.

RESULTS

Extracts and enzymic hydrolysates, prepared according to the methods described above, were subjected to careful analysis for a number of organic and inorganic constituents. Table I lists the yields and properties of the preparations; in Table II the analytical methods used are given. Tables III and IV give the results of determinations of moisture, ash, cobalt, fluorine, total nitrogen, amino-nitrogen, choline, thiamine, riboflavin, folic acid, niacin, pantothenic acid and vitamin B₁₂.

DISCUSSION

Enzymic digestion of liver or liver residue was done to render the proteins soluble in water. The effectiveness of papain digestion was tested by determining, at hourly intervals, the total solids and the amino-nitrogen content of hydrolysates (Fig. 2). It was found that after 5 hours of digestion, a maximum was

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TABLE I. Review of extracts and hydrolysates.

No.	Raw material	Details of procedure ^a	Yield in dry matter	Properties
Extracts			%	
1.	Cod liver residue	—	10	All yellow, all hygroscopic
2.	Same	+	7	
3.	Salmon liver frozen	+	7	
4.	Pork liver, dried, defatted	—	27	
5.	Same	+	22	
6.	Beef liver, dried, defatted	—	28	
7.	Same	+	20	
ENZYMIC HYDROLYSATES				
8.	Cod liver residue, dried and defatted	Standard method	86	Yellow-brown
9.	Same	Same	65	Brown
10.	Cod liver, whole	Hydrolysis with papain only; oil removed after hydrolysis	..	Bright yellow, slightly fishy smell
11.	Haddock liver residue, dried and defatted	Standard method	65	Brown, slightly hygroscopic
12.	Salmon liver, dried and defatted	Same	73	Dark brown
13.	Whale liver, dried and defatted	Same	78	Dark brown
14.	Seal liver, frozen	Hydrolysis with papain only	..	Dark brown
15.	Pork liver, dried and defatted	Standard method	76	Brown, slightly bitter taste
16.	Beef liver, dried and defatted	Same	71	Same

^aA + in this column indicates that the concentrate was treated with 95% ethanol; a — indicates absence of this treatment.

TABLE II. Methods used in the analysis of liver extracts and enzymic hydrolysates⁴.

Constituent	Method	Reference
Water	12 hr. at 85–90° C. and 2 hr. at 110° C.	...
Ash	At 500° C.	...
Calcium	In ash as oxalate	...
Phosphorus	Berenblum and Chain	<i>Biochem. J.</i> 32: 295 (1938)
Copper	Parker and Griffin	<i>Can. J. Res.</i> , B, 17: 66 (1939)
Iron	Same	Same
Cobalt ⁴	McIntire	<i>J.A.O.A.C.</i> 34: 597 (1951)
Fluorine ⁴	Same	Same
N-total	Kjeldahl	...
N-NH ₂	Spies and Chambers	<i>J. Biol. Chem.</i> , 191: 787 (1951)
Choline	U.S.P.	<i>U.S.P. XII</i> , First Bound Supplement (1943)
Thiamine	<i>Lactobacillus fermenti</i> , Sarett and Cheldelin	<i>J. Biol. Chem.</i> , 155: 153 (1944)
Riboflavin	<i>Lactobacillus casei</i> , U.S.P.	<i>U.S.P. XII</i> , First Bound Supplement (1943)
Folic acid	<i>Lactobacillus casei</i> , Teply and Elvehjem	<i>J. Biol. Chem.</i> , 157: 303 (1945)
Niacin	<i>Lactobacillus arabinosus</i> , U.S.P.	<i>U.S.P. XII</i> , First Bound Supplement (1943)
Pantothenic acid	<i>Lactobacillus arabinosus</i> , Skeggs and Wright	<i>J. Biol. Chem.</i> 156: 21 (1944)
Vitamin B ₁₂	<i>Lactobacillus leichmannii</i> , Peeler <i>et al.</i>	<i>Proc. Soc. Exp. Biol. Med.</i> , 72: 515 (1949)

⁴Analyses done by Mr. W. M. Langille, Department of Agriculture, Truro, Nova Scotia.

TABLE III. Inorganic constituents of liver extracts and enzymic hydrolysates calculated on a water-free basis.

No.	Raw material	Ash	Cal- cium	Phosphorus			Copper	Iron	Cobalt	Fluo- rine	
				Inor- ganic	Organic (calcu- lated)						Total
					%	%					
	EXTRACT	%	%	%	%	%	μg./g.	μg./g.	μg./g.	μg./g.	
1.	Cod liver residue	9.03	0.098	0.59	1.26	1.85	342	162	
2.	Same	11.40	0.045	0.60	1.41	2.01	121	50.4	
3.	Salmon liver frozen	8.77	0.085	0.77	0.75	1.52	131	156	
4.	Pork liver, dried, defatted	15.20	0.166	1.63	0.64	2.27	355	162	
5.	Same	14.10	0.083	1.25	0.50	1.75	141	55	
6.	Beef liver, dried, defatted	13.47	0.064	1.44	0.60	2.04	397	145	
7.	Same	13.50	0.054	1.23	0.80	2.03	135	29	
ENZYMIC HYDROLYSATES											
8.	Cod liver residue, dried and defatted	6.75	0.067	0.29	1.34	2.63	74	64	0.44	305	
9.	Same	10.28	0.085	0.53	1.50	2.03	78	158	0.92	100	
10.	Cod liver whole	6.90	0.039	0.42	1.25	1.67	45	135	
11.	Haddock liver residue, dried and defatted	10.16	...	0.43	79	160	2.57	203	
12.	Salmon liver, dried and defatted	7.78	0.092	0.73	0.76	1.49	0.70	646	
13.	Whale liver, dried and defatted	5.98	0.050	0.44	0.46	0.90	254	236	0.63	310	
14.	Seal liver, frozen	5.20	0.034	0.58	0.24	0.82	63	114	...	180	
15.	Pork liver, dried and defatted	7.67	0.063	0.59	0.27	0.86	150	167	0.66	130	
16.	Beef liver, dried and defatted	8.00	0.049	0.56	0.48	1.04	178	74	0.33	250	

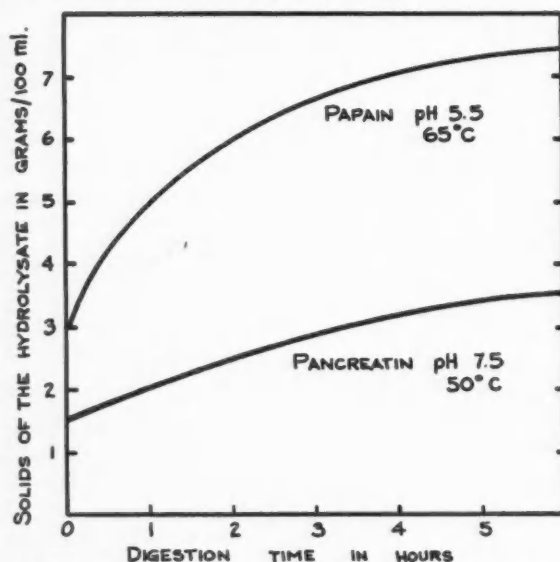


FIGURE 2. Effect of papain and pancreatin treatment on solid content of salmon liver hydrolysate.

TABLE IV. Organic constituents of liver extracts and enzymic hydrolysates calculated on a water-free basis.

No.	Raw material	Total nitrogen	NH ₂ nitrogen	Choline base	Thiamine	Ribo- flavin	Folic acid	Niacin	Panto- thenic acid	Vitamin B ₁₂
	EXTRACTS	%	%	%	μg./g.	μg./g.	μg./g.	μg./g.	μg./g.	μg./g.
1.	Cod liver residue	7.40	2.50	2.54	2.44	40.4	11.8	425	136	4.70
2.	Same	9.60	4.00	3.34	2.12	65.8	15.3	573	212	1.90
3.	Salmon liver frozen	11.60	5.56	0.96	7.02	55.0	7.02	581	184	2.20
4.	Pork liver, dried, defatted	9.50	4.78	5.94	9.86	433.0	19.00	1664	606	3.42
5.	Same	9.28	4.87	4.87	10.90	419.0	...	1856	614	2.78
6.	Beef liver, dried, defatted	7.67	3.12	3.32	8.06	313.0	14.50	2062	530	12.90
7.	Same	8.14	4.99	2.78	8.50	323.0	22.12	2619	698	4.50
	ENZYMIC HYDROLYSATES									
8.	Cod liver residue, dried and defatted	7.98	3.54	1.10	7.40	35.0	9.80	247	86	0.48
9.	Same	12.87	5.27	1.26	2.95	101.0	10.50	369	89	3.80
10.	Cod liver whole	12.04	5.30	1.26	1.50	71.0	9.00	366	91	2.51
11.	Haddock liver residue, dried and defatted	11.05	5.02	2.24	1.61	73.0	15.80	321	57	0.86
12.	Salmon liver, dried and defatted	12.60	5.57	1.31	8.90	61.0	7.50	262	79	4.80
13.	Whale liver, dried and defatted	10.96	5.31	1.06	9.64	91.0	3.40	433	148	2.15
14.	Seal liver, frozen	14.6	7.22	0.24	5.30	106.0	8.20	493	342	1.27
15.	Pork liver, dried, defatted	12.30	6.23	1.86	4.48	131.0	6.48	616	231	1.35
16.	Beef liver, dried, defatted	11.1	5.72	1.75	3.92	138.0	6.54	888	261	4.79

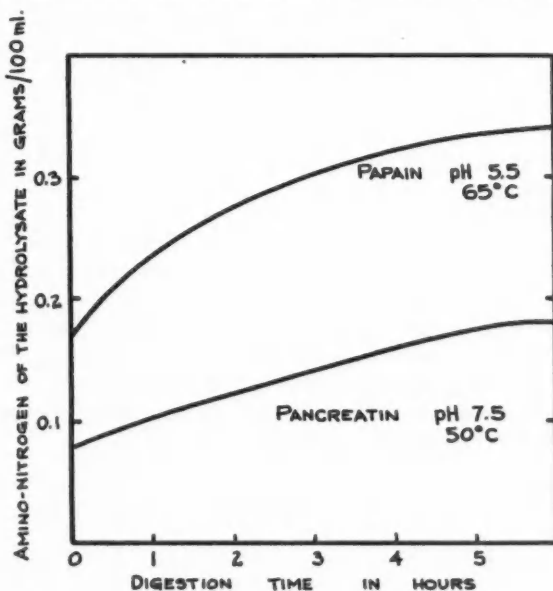


FIGURE 3. Effect of papain and pancreatin treatment on amino-nitrogen content of salmon liver hydrolysate.

reached, and that prolongation of the enzyme treatment did not cause a further increase in solids or amino-nitrogen of the hydrolysates.

Pancreatin digestion of the residue of the papain treatment (Fig. 3) further increased the total solids and amino-nitrogen content of hydrolysates during the first hour of treatment. Thereafter, the solid content continued to increase, until a maximum was reached after about 4 hours.

Four hours of papain treatment followed by 3 hours of pancreatin digestion were chosen as the standard procedure in preparing the digests.

An over-all comparison of the properties of extracts and digests (Table I) shows two major differences. First, the yields (percentage of dry material from liver residue, obtained in the final preparation) were much higher for digests than for extracts. Second, all extracts were very hygroscopic, whereas the digests attracted moisture not at all or only very slightly. The vitamin content of enzymic hydrolysates was, as a rule, lower than that of extracts (Table IV), but the total vitamin yield was much higher with hydrolysates than with extracts made from the same raw material.

Comparison of the amounts of organic and inorganic constituents in products from fish livers with similar products from mammalian livers (Table III) shows that preparations made from cod and haddock liver usually contain less than beef or pork liver extracts or hydrolysates. A special position was held by preparations from salmon (*Salmo salar*) liver; they compared very favourably with products from beef and pork livers.

Salmon liver, compared with other fish livers, was a very attractive raw material, since its low oil content allowed enzymic digestion and removal of oil in one operation, rather than in two separate procedures.

CONCLUSIONS

1. Extracts and enzymic hydrolysates with good nutritive qualities can be prepared from fish livers; salmon liver is a most attractive raw material but cod and haddock livers are also very suitable.
2. Fish liver extracts and hydrolysates can be used for the same purposes as similar preparations from mammalian livers: in nutrition, as additives to diets; and in medicine.
3. Further study of processes for large scale production of these preparations is required. Pilot plant experiments are now being started in this laboratory and a study of possible markets for these products is necessary before a final decision about economical applicability of extracts and enzymic hydrolysates from fish livers can be reached.

ACKNOWLEDGMENT

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Note on Albumin Protein Fractions in a Sturgeon^{1, 2}

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ABSTRACT

The muscle of a sturgeon taken off Nova Scotia contained no trimethylamine oxide. The electrophoretic pattern of the water-soluble proteins indicates at least 10 non-dialysable components in the extract, two of which have weak positive mobilities.

RECENTLY the proteins extractable at low ionic strength have been investigated electrophoretically in several species of fish: Hamoir (1951), Connell (1953a,b), Dingle *et al.* (1955).

The availability of a live sturgeon allowed us to investigate a species of this branch of the Teleostomi, the Chondrostei, as contrasted with the Teleostei (Breder, 1948). The specimen used was first identified as a short-nosed sturgeon, *Acipenser brevirostrum* (LeSueur, 1818), but further study indicates that it is probably an abnormal specimen of sea sturgeon, *A. oxyrhynchus* (Mitchill, 1815).

The specimen examined was 80 cm. in length. Portions of the back muscle were removed for analysis. The results, using methods as previously described (Dyer *et al.*, 1950; Dyer, 1952), were as follows: moisture, 77.8 per cent; fat (by ether extraction of the dried muscle), 6.2 per cent; total nitrogen, 2.27 per cent; non-protein nitrogen, 0.34 per cent. This gives a protein nitrogen content of 1.93 per cent, as compared to 2.5 per cent for cod (*Gadus callarias*). The muscle contained no trimethylamine or trimethylamine oxide, in agreement with other anadromous fish (Dyer, 1952), although this specimen was caught in salt water (St. Margaret's Bay, Nova Scotia).

The composition of a water extract of the muscle was investigated by electrophoresis, as previously described (Dingle *et al.*, 1955). The sample was stored at 0°C. until rigor mortis had passed, then was cut into small pieces and extracted with an equal weight of cold water for six hours. The resulting solution was dialysed against three changes of a phosphate buffer containing 0.10 M sodium chloride, with a total ionic strength of 0.15 and pH 6.52. The descending pattern obtained in this buffer is shown in the Figure. The peaks are numbered arbitrarily, in descending order of mobility. There was some turbidity in the sample, but this migrated rapidly out of the electrophoresis cell.

There appear to be at least ten non-dialysable components in the extract, and all but two possessed negative mobilities. The immobile peak probably represents an eleventh component as well as the boundary anomaly. The pattern

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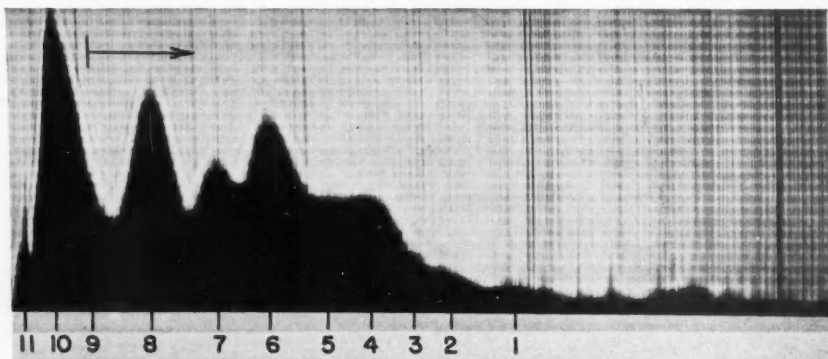


FIGURE 1. Electrophoresis pattern (descending limb) of a water extract of the muscle of short-nosed sturgeon. (Ionic strength = 0.15; pH = 6.52; 2.48 mg. protein N/ml.; 8.7 volt/cm.; 17,200 sec.)

does not closely resemble any of those obtained by Connell (1953b) for extracts of 20 different fishes. His data indicated that only the lower fishes such as skates have water-extractable components with positive mobilities at a pH of 7.5. The occurrence of two components (10 and 11) with weak positive mobilities in our sturgeon extract agrees with the usual classification of these fish as intermediate between the elasmobranchs and the true fishes. The isoelectric points of these two components must be slightly higher than pH 6.5, whereas we had previously found that the highest isoelectric point of a similar cod extract was about 5.9 (Dingle *et al.*, 1955).

Mobilities calculated from the electrophoresis pattern are given in the Table. Approximate Gaussian curves were fitted to the pattern in an effort to locate the

TABLE I. Relative amount and electrophoretic mobilities of the components of a water extract of muscle of short-nosed sturgeon

Peak number	Percentage of total area	Mobility ^a $\left(\frac{\text{cm}^2}{\text{volt-sec.}} \times 10^5 \right)$
1	1.4	-2.51
2	2.2	-2.11
3	1.9	-1.88
4	9.5	-1.64
5	8.6	-1.36
6	17.6	-1.03
7	9.8	-0.72
8	22.5	-0.36
9 ^b	6.6	0
10	18.2	+0.19
11	1.4	+0.37

^aIonic strength, 0.15; pH, 6.52.

^bShould include the ϵ peak which would probably be smaller than the percentage indicated.

peaks due to the different components, and to obtain a rough idea of their relative amounts. The resulting percentage composition of the extract is also given in the Table.

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Estimation of Recruitment and Natural Mortality Rate from Age-Composition and Catch Data in British Columbia Herring Populations¹

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ABSTRACT

If absolute recruitment (R) and natural mortality rate (q) are both presumed constant in each of two or more periods of stabilized fishing, it is shown that $i = q + (1/R)iC$, where i is instantaneous total mortality rate and C is catch in numbers. The relationship yields approximate estimates of R and q under semi-stable conditions if "average referable C " is related to apparent i , the former derived from catch data and the latter from age-composition data for post-recruited age-groups. In the herring population, in which recruitment takes place mostly at age III but is spread from ages I to IV, the average of the catch of years x and $x + 1$ is referable to apparent i at ages IV to V in year $x + 2$, at ages V to VI in year $x + 3$, etc. When q increases with advancing age, it is shown that R is most accurately estimated from data for ages IV to V; q is slightly overestimated at ages IV to V and underestimated at ages VI to VII and VII to VIII. From data for periods of approximate stability in the lower east coast of Vancouver Island population, average R is estimated at about 500 million fish per year; average q appears to increase with age, ranging from about 0.4 at ages IV to V to about 0.85 at ages VII to VIII. For a recent period of stabilized intensive fishing, a rough estimate of the average initial size of the fishable stock, based on age-composition and catch data, agrees well with that estimated by another method. For populations along the west coast of Vancouver Island, q also appears to increase with advancing age; R is estimated at about 400 million fish. In an appendix it is shown that a method of estimating q from age-composition and effort data gives unsatisfactory results because effort expended in herring fishing is not proportional to rate of fishing of the stock.

INTRODUCTION

RICKER (1948), Beverton and Holt (1954), and others have discussed the "catch curve", a plot of the logarithm of number of fish against age in samples of catch, and its use in estimating total annual or instantaneous mortality rates or coefficients. Under conditions of approximately stable recruitment and fishing effort over a period of years, the nature of recruitment in respect to age may be determined from the left-hand limb and dome of the curve, and the survival or mortality rate may be determined from the slope of the right-hand limb. Both authors have discussed factors producing curvature of the right-hand limb, the most obvious of which is a secular change in rate of fishing. Given two periods of stabilized fishing in which effort is similar within periods but different between periods, and adopting the assumption that natural mortality rate is constant, Silliman (1943) has shown that total mortality rate may be segregated into its two components, natural and fishing mortality rates, and that the average

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numerical magnitude of both the annually recruited fish and the stock may be estimated from age-composition, catch and effort data. In addition, Beverton (1954) and Beverton and Holt (1954) have shown that natural and fishing mortality rates may be estimated from age-composition and effort data when effort is changing from year to year.

Data on age-composition, catch and effort are available over a long period of years for the herring populations of the lower east coast and west coast of Vancouver Island sub-districts. Unfortunately, for reasons which will be discussed later, effort is not necessarily proportional to rate of fishing. This deficiency greatly restricts the usefulness of age-composition and catch data in estimating the vital statistics of the population. However it is considered worth while to examine the data in some detail to determine the nature of recruitment, to estimate total mortality rates under various fishing pressures and, if possible, to estimate natural mortality rate, fishing mortality rate, average number of recruits and average size of the fishable stock, even though these may be but rough approximations to the true values.

METHODS

Theoretical vital statistics developed by Ricker (1948, p. 4; and elsewhere) were investigated to see if, during two periods of equilibrium under different fishing pressures, it might not be possible to estimate both absolute numerical recruitment and natural mortality rate from knowledge only of age-composition and catch. As will be shown below, this may be done if it is assumed that (1) absolute recruitment and (2) natural mortality rate are both constant in time. The first assumption, while certainly not true from year to year, must be true over a long period of years, otherwise population abundance would either increase to infinity or decrease to zero. However the existence of cycles of abundance in certain populations shows that long-term trends in recruitment may take place and indicates the need for caution. The second assumption, applying only to post-recruited fish, may be accepted as reasonable pending evidence to the contrary; it must also be adopted in using statistics of effort and catch (Silliman, 1943, p. 4).

It is further assumed that the herring population conforms to Type IB (Ricker, 1944, p. 27) with recruitment taking place abruptly just prior to the start of the fishing season and with both natural and fishing mortality rates applying during the fishing season.³

Let the following constants obtain during a period of equilibrium:

- a = annual rate of total mortality
- p = instantaneous rate of fishing mortality
- q = instantaneous rate of natural mortality
- $i = p + q$ = instantaneous rate of total mortality
- $u = ap/i$ = rate of exploitation

³The author is indebted to Dr. W. E. Ricker, Pacific Biological Station, Nanaimo, B.C., for investigating the situation in which natural mortality is assumed to be absent during

R = number of recruits (hence also the number of yearly deaths)

$N = R/a$ = initial population number

$C = Nu$ = catch

The following relationships will apply:

$$C = Nu = Nap/i = Rp/i = R(i - q)/i$$

Hence:

$$i = q + (1/R)iC \quad (1)$$

If both R and q are presumed constant during two or more periods of equilibrium, each period with a different i and C , a straight-line relationship will exist between i and iC . The slope will be the reciprocal of the number of recruits. The intercept on the i axis when $iC = 0$ will be the instantaneous natural mortality rate, q .

If only two equilibrium periods are involved the following simultaneous equations result:

$$\begin{aligned} i_1 &= q + (1/R)i_1C_1 \\ i_2 &= q + (1/R)i_2C_2 \end{aligned}$$

Solving for R and q :

$$R = \frac{i_1C_1 - i_2C_2}{i_1 - i_2} \quad (2)$$

$$q = i_1 - \frac{i_1C_1}{R} \quad (3)$$

For each period of equilibrium, an estimate of i may be obtained from age-composition data at and beyond the last age at which recruits are added to the fishable stock. For example, if recruitment is completed at age IV and the age-composition of the catch shows 30 per cent of the fish at age IV and 15 per cent at age V, the survival rate ($s = 1 - a$) is 15/30, or 0.50. From the relationship

the fishing season. In this, the seasonal rate of fishing m becomes the rate of exploitation u . Thus, using symbols explained in the text and following the same argument:

$$m = u = 1 - e^{-p} = 1 - e^{-(i-q)} = Ca/R \quad (A)$$

Hence, for two periods of equilibrium:

$$i_1 - i_2 = -\log_e(1 - C_1a_1/R) + \log_e(1 - C_2a_2/R) \quad (B)$$

Equation B may be solved for R , given C and i in two periods of equilibrium, as follows:

$$R = \frac{e^{i_1-i_2}C_1a_1C_2a_2}{e^{i_1-i_2} - 1}$$

Knowing R , q may be found by substitution of one set of values of i , C , and a in equation A. Application of these formulae to data to be presented later results in a slightly higher estimate of q and a lower estimate of R as compared with those obtained with formulae developed in the text. Ricker suggests that the true distribution of natural mortality may be somewhere between the two assumptions, that is, that it occurs both during the fishing season and at other times of the year.

$s = e^{-i}$, i may be determined either as the natural logarithm of s (with sign changed) or from Ricker's (1948, pp. 98-101) tables, as 0.693. Alternatively, if the catch curve shows a straight right-hand limb, s may be found as the anti-logarithm of the slope of the best straight line relating the common logarithm of the number at each age (Y), to age (X).

As Ricker (1948, p. 18) has pointed out, the mortality rates derived from age-composition pertain to past years, i.e. to the years during which the year-classes were being recruited. This lag must be taken into consideration in relating catch and mortality rate in the formulae. The extent of the lag will depend on the nature of recruitment. Assume that an equilibrium condition is reached in year x and persists thereafter. If recruitment takes place abruptly at one age, say IV, the definitive mortality rate of the equilibrium (referable to the catch in year x) will appear at ages IV to V in year $x + 1$, at ages V to VI in year $x + 2$, etc. If recruitment is spread over four age-groups, say I to IV, the definitive mortality rate of the equilibrium will appear at ages IV to V in year $x + 4$, at ages V to VI in year $x + 5$, etc.

As a rigid equilibrium will never be attained in practice, it is worth while to determine how changing annual mortality rates are reproduced in the age structure of a mathematical model resembling the lower east coast of Vancouver Island population. As will be determined later, average annual recruitment (say, $R = 10,000$) is spread throughout ages I to IV in the following relative numbers: $R_1 = 42$, $R_2 = 749$, $R_3 = 7,493$, $R_4 = 1,717$. The population, shown in part in Table I, starts at equilibrium with an annual mortality rate (a) of 0.80 and is subjected in subsequent years to annual rates of 0.75, 0.70, 0.65 and 0.60. It will be noted that the lag in time between the application of a mortality rate and its appearance in age structure is different for each age-group of recruits. Thus in year 5 the rates determined at ages IV to V for R_1 (0.80), R_2 (0.75), R_3 (0.70) and R_4 (0.65) are the rates which applied 4, 3, 2 and 1 years previously, i.e. in years 1, 2, 3 and 4. The composite rate (0.6815), which will be the only rate measurable in practice, is a weighted average of the rates of the four previous years, the weighting factors being the number of survivors of each recruited group at age IV. As the weighting factors change from year to year when mortality rate is changing, it will be impossible to recover the true rate for any given year from age-composition data. It will be noted, however, that the composite or apparent mortality rate determined in the several years at age IV to V is influenced chiefly and almost equally by the rates which obtained in the two previous years. Thus in year 3, 0.7763 approximates the average (0.775) of the rate applying in year 1 (0.80) and year 2 (0.75); in year 4, 0.7294 approximates the average (0.725) of the rate applying in year 2 (0.75) and year 3 (0.70). This suggests that in attempting to utilize the relationship between i and C under non-equilibrium conditions, apparent i as measured from age-composition at ages IV to V in year 3 should be related to the average catch of years 1 and 2; similarly apparent i at ages IV to V in year 4 should be related to the average catch of years 2 and 3. Extending the above argument, it follows that the average catch of years x and $x + 1$ is referable to the apparent i at ages IV to V

TABLE I. Model (in part) of a population with recruitment spread from ages I to IV, which starts at equilibrium and undergoes successively changing mortality rates (a). The rates determined from the number of survivors at ages IV and V and at ages V and VI are given in brackets.

Start of year	a during year	Relative numbers in initial population and catch at ages							
		I	II	III	IV	(a)	V	(a)	VI
1 and earlier	0.80	42	757.40	7644.48	3245.90	(0.8000)	649.180	(0.8000)	129.8360
		42	8.4	1.68	0.34	(0.80)	0.068	(0.80)	0.0136
			749	149.8	29.96	(0.80)	5.992	(0.80)	1.1984
				7493	1498.6	(0.80)	299.72	(0.80)	59.944
					1717	(0.80)	343.4	(0.80)	68.68
2	0.75	42	757.40	7644.48	3245.90	(0.8000)	649.180	(0.8000)	129.8360
		42	10.5	2.10	0.42	(0.80)	0.085	(0.80)	0.017
			749	187.25	37.45	(0.80)	7.49	(0.80)	1.498
				7493	1873.25	(0.80)	374.65	(0.80)	74.93
					1717	(0.75)	429.25	(0.80)	85.85
3	0.70	42	759.5	7682.35	3628.12	(0.7763)	811.475	(0.8000)	162.295
		42	12.6	3.15	6.63	(0.80)	0.126	(0.80)	0.0255
			749	224.70	56.175	(0.80)	11.235	(0.80)	2.247
				7493	2247.9	(0.75)	561.975	(0.80)	112.395
					1717	(0.70)	515.1	(0.75)	128.775
4	0.65	42	761.60	7720.85	4021.705	(0.7294)	1088.436	(0.7763)	243.4425
		42	14.7	4.41	1.102	(0.80)	0.2205	(0.80)	0.0441
			749	262.15	78.645	(0.75)	19.6612	(0.80)	3.9322
				7493	2622.55	(0.70)	786.765	(0.75)	196.6912
					1717	(0.65)	600.95	(0.70)	180.295
5	0.60	42	763.70	7759.56	4419.297	(0.6815)	1407.5967	(0.7294)	380.9525

in year $x + 2$, at ages V to VI in year $x + 3$, at ages VI to VII in year $x + 4$, and at ages VII to VIII in year $x + 5$. It may be noted that fish of successive ages in successive years belong to the same year-class. Thus the average catch of years x and $x + 1$, henceforth called the "average referable catch", can be related to the apparent mortality rate determined from a pair of adjacent year-classes at several ages in successive years. It should be stressed that this approximation is intended to apply only to the population presently under consideration. Other approximations could be determined for those populations with a different spread in recruitment.

The mathematical model was further investigated to determine to what extent estimates of R and q would be biased by the above approximation under rather extreme downward and upward trends in total mortality rate. The total mortality rate (a) was varied from 0.80 at equilibrium through the following rates in successive years: 0.80, 0.75, 0.70, 0.65, 0.60, 0.60, 0.65, 0.70, 0.75 and, thereafter, 0.80. Assuming a constant natural mortality rate of $q = 0.75$, catch, average referable catch and apparent i were determined for each year. Using equations 2 and 3, calculations of apparent R and apparent q were made by

comparing average referable catches and apparent total mortality rates in each successive year with those under equilibrium conditions. From the results, summarized in Table II, it may be seen that both R and q are overestimated as a (and i) decreases and underestimated as it increases. They are fairly close to the true values ($R = 10,000$; $q = 0.75$) when the average referable catch reaches a "low" (year 7). The ranges of apparent R (8,213 to 12,272) and q (0.563 to 0.909) are less than might be expected, and indicate the possibility of obtaining approximately accurate estimates even when rate of total mortality (and thus, rate of fishing) is changing. This will be particularly true when data referable to a "low" between two "highs" are available.

An average estimate of R and q may be obtained by applying equation 1 to the data of years 1 to 10 inclusive (the period of changing total mortality rates), obtaining the line of best fit between i and iC by least squares. When this is done, $R = 10,216$ and $q = 0.768$ (true values are 10,000 and 0.75, respectively). The over- and underestimates of R and q , noted above in comparing the data for each year with those under equilibrium conditions, tend to average out. Again the results indicate the possibility of obtaining approximately accurate estimates of R and q under non-equilibrium conditions provided there is no overall upward or downward trend in catch and thus, presumably, in rate of fishing and total mortality rate, over the period under consideration.

Finally it might be noted that the estimation of R and q becomes more difficult if natural mortality rate increases progressively with age. This may be illustrated by setting up a mathematical model with recruitment spread from ages I to IV as before, and with q progressively increasing at ages I to II, II to III, III to IV, etc., as follows: 0.25, 0.30, 0.35, etc. If these changing rates of natural mortality are combined with constant rates of fishing, $p_1 = 0.40$ and $p_2 = 0.80$ in equilibrium periods 1 and 2, the initial populations may be calculated as 18,294 (N_1) and 14,470 (N_2) fish. Applying a different rate of exploitation (u) at each age, the catches become 5,055 (C_1) and 6,809 (C_2).

TABLE II. Data pertaining to a theoretical population undergoing changing total mortality rates, with recruitment (10,000 fish per year) spread over ages I to IV and with an assumed natural mortality rate of $q = 0.75$.

Year	True a	Apparent a (ages IV-V)	Apparent i	N	True u	Catch	Average referable catch	Apparent	
								R	q
1 and earlier	0.80	0.8000	1.6094	12500	0.4272	5340	5340
2	0.75	0.8000	1.6094	12500	0.3442	4303	5340
3	0.70	0.7763	1.4975	13126	0.2640	3465	4822	12,272	0.9091
4	0.65	0.7294	1.3071	13939	0.1856	2587	3884	11,635	0.8708
5	0.60	0.6815	1.1441	14880	0.1089	1620	3026	11,030	0.8302
6	0.60	0.6333	1.0032	15953	0.1089	1737	2104	10,695	0.8058
7	0.65	0.6013	0.9196	16382	0.1856	3040	1678	10,222	0.7686
8	0.70	0.6193	0.9658	15735	0.2640	4154	2388	9,770	0.7297
9	0.75	0.6702	1.1092	14721	0.3442	5067	3597	9,205	0.6758
10	0.80	0.7227	1.2826	13681	0.4272	5844	4608	8,213	0.5630
11	0.80	0.7758	1.4952	12737	0.4272	5441	5455
12	0.80	0.8020	1.6195	12590	0.4272	5378	5642

To estimate q at each age comparison, it is necessary to know not only C_1 and C_2 over all ages, but also i_1 and i_2 at each age comparison. Now, however, the estimate of i will change from the true rate as determined from age-composition of the initial population to a larger apparent rate as determined from the age-composition of the total catch. If sampling is distributed uniformly throughout the fishing season, i as determined from the average age-composition of the samples may be assumed to be an average of the initial true and final apparent rate. Thus for period 1, the values of average apparent i at ages IV to V, V to VI, VI to VII, and VII to VIII become 0.8108, 0.8608, 0.9105 and 0.9606 (true values are 0.80, 0.85, 0.90 and 0.95). For period 2 they become 1.2100, 1.2599, 1.3098 and 1.3597 (true values are 1.20, 1.25, 1.30 and 1.35). Equations 2 and 3 yield estimates of R of 10,372, 10,592, 10,809 and 11,031 fish, whereas the true value is 10,000 fish. Estimates of q become 0.4157, 0.4500, 0.4847 and 0.5205, whereas the true values are 0.40, 0.45, 0.50 and 0.55. Thus, when natural mortality rate is progressively increasing with age, there is a progressively greater overestimation of R at successive age comparisons; the best estimate, which is still larger than the true value, is obtained from data pertaining to the youngest age-groups after recruitment is completed, i.e. at ages IV to V in the model. On the other hand, q is overestimated at the younger and underestimated at the older age comparisons; the best estimate (exact in the model) is from data pertaining to ages V and VI.

The estimation of recruitment and natural mortality from age-composition and catch data will be further complicated by annual fluctuations in recruitment. Fortunately in the British Columbia herring populations these may be classed as "moderate". It can be hoped that they will average out over a period of years and thus not greatly influence the average estimates of R and q .

MATERIAL

BACKGROUND

The herring of the lower east coast and west coast of Vancouver Island are fished by purse seines during the autumn and winter of each year. In the former sub-district fishing takes place in Areas 17 and 18; in the latter, it takes place in Areas 23 to 27 (Fig. 1). The history of the herring fishery in both sub-districts up to 1933-34, including a discussion of life history, fishing methods, catch and marketed products, has been given by Tester (1935). That of the west coast of Vancouver Island up to 1945-46 has been summarized by Tester (1948), and each year since that time it has been reviewed in a series of articles by various authors which are published annually in the *Report of the British Columbia Fisheries Department*. Since 1945-46, the two sub-districts have been subjected to an experiment in herring management. The lower east coast has been maintained on a quota of 40,000 tons (extended or exceeded in some years) whereas the west coast has had no quota and the catch has been limited only by a closing date (February 5). The results of the experiment are discussed by Stevenson and Outram (1953).

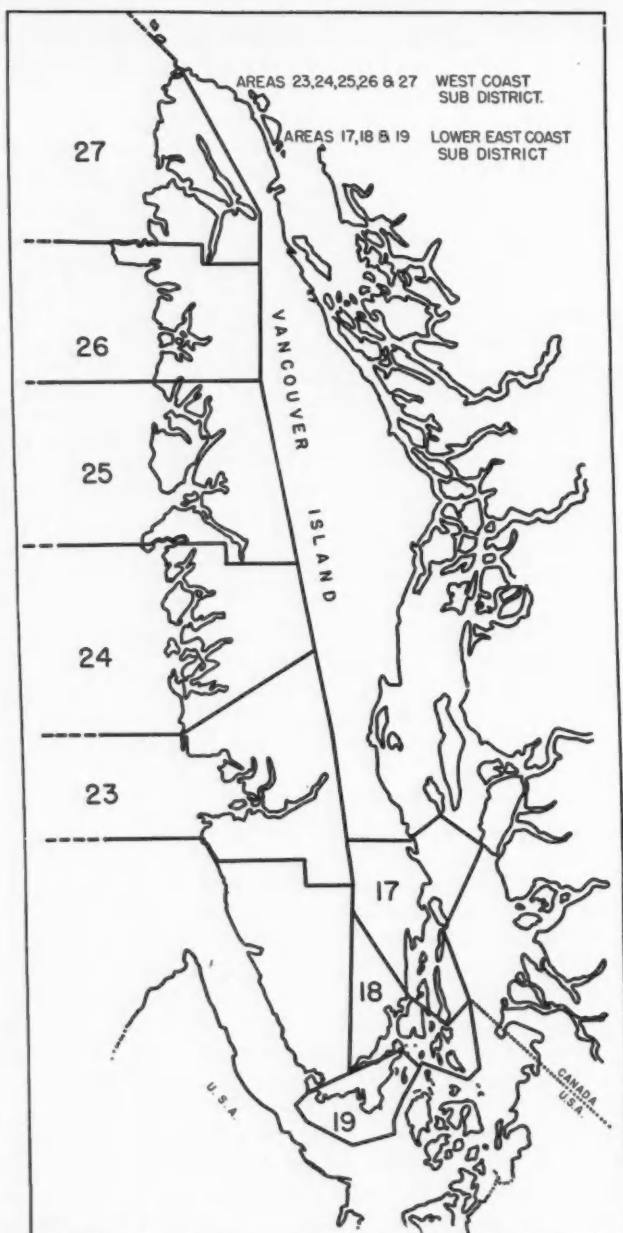


FIGURE 1. Map showing the location of statistical sub-districts and areas in the vicinity of Vancouver Island.

POPULATIONS

The run to the lower east coast of Vancouver Island is considered to comprise one more or less discrete population and is dealt with as a unit here.

The runs to the five areas on the west coast of Vancouver Island appear to constitute a series of intergrading populations, although they were treated as one large population by Tester (1948) in appraising the efficacy of the quota system of catch regulation. Recently, Stevenson (1954) has summarized all available tagging data and has suggested that the populations might be segregated into two more or less separate units, a southern population comprising the runs to Areas 23 and 24, and a northern population comprising the runs to Areas 25, 26 and 27. As will be seen later, the age-composition of Area 27 differs considerably from that of all other west coast areas, indicating that it might be regarded as a third unit. Accordingly in the present study, three west coast of Vancouver Island units are dealt with separately: Area 23-24, Area 25-26, and Area 27. In addition, however, consideration is given to the combined data of the first two: Area 23-26.

CATCH

Annual catches in thousands of tons are included in Tables III, VIII, IX and X and are shown graphically in Figures 2 and 5. The catch by weight is derived from sources discussed by Tester (1945, pp. 10-15). Over most of the

TABLE III. Total catch for the lower east coast sub-district over the period 1906-07 to 1953-54 in terms of weight (thousands of tons) and number (millions of fish).

Year	Catch		Year	Catch	
	Weight	Number		Weight	Number
1906-07	4.3 ^a	...	1930	34.6	345
1907-08	9.6 ^a	...	1931	42.6	420
1908-09	21.7 ^a	...	1932	14.3	138
1909-10	27.8 ^a	...	1933-34	28.2	290
1910-11	8.8	82 ^b	1934-35	16.7	157
1911-12	22.4	208 ^b	1935-36	17.1	153
1912-13	23.5	218 ^b	1936-37	24.7	237
1913-14	25.4	236 ^b	1937-38	25.1	259
1914-15	18.9	175 ^b	1938-39	26.3	268
1915-16	15.2	134	1939-40	32.3	315
1916-17	16.1	150	1940-41	31.9	299
1917	15.2	142	1941-42	48.9	465
1918	13.1	129	1942-43	43.9	463
1919	3.9	35	1943-44	42.4	411
1920	15.3	142 ^b	1944-45	39.5	382
1921	20.2	191	1945-46	40.0	371
1922	25.4	240	1946-47	36.5	336
1923	15.7	142 ^b	1947-48	39.9	336
1924	18.2	174	1948-49	40.1	405
1925	37.4	343	1949-50	40.3	373
1926	37.5	360 ^b	1950-51	41.0	380
1927	34.2	328 ^b	1951-52	41.0	344
1928	46.2	443 ^b	1952-53	8.1	87
1929	43.5	421	1953-54	52.7	488

^aIncludes salted fish not converted to fresh.

^bEstimated.

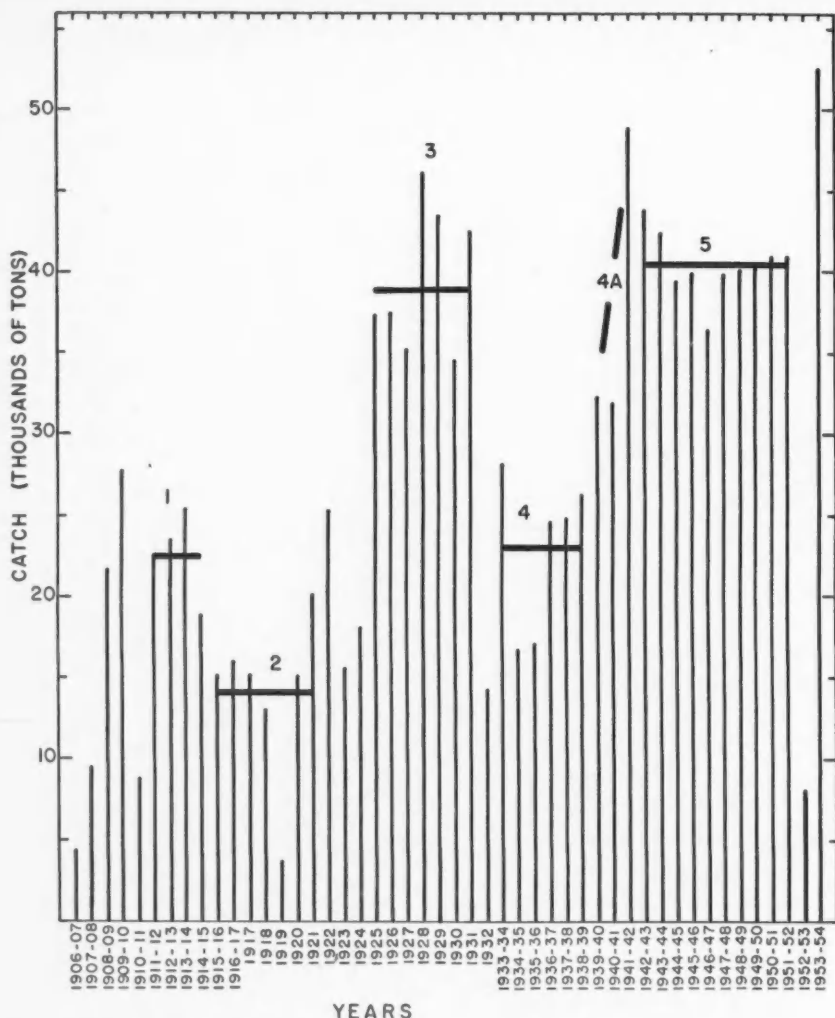


FIGURE 2. Catch of herring in the lower east coast sub-district from 1906-07 to 1953-54, with five periods of approximately stable catch indicated by horizontal bars.

period the statistics are compiled for the fishing season which may include the last part of one calendar year and the first part of the next. From 1917 to 1932 statistics are available only for the calendar year. These have been taken as representative of the catch during the fishing season, even though a slight error is involved. As the catch data are averaged in subsequent treatment, the error is minimized.

Annual catches in millions of fish are also included in the tables. They have been calculated from a consideration of the catch in tons, the age-composition derived from samples, and the average weight of the fish at each age. In years in which age-compositions are not available, the catch in numbers is estimated from the catch in weight with due consideration of the age-compositions and average weights of the nearest years with complete data.

SAMPLING

Sampling data are available from the lower east coast of Vancouver Island sub-district from 1915-16 to 1953-54, except for 1920-21, 1923-24, and 1926-27 to 1928-29. For the west coast of Vancouver Island sub-district they are available from 1929-30 to 1953-54, although there are gaps in the data for Area 25-26 and Area 27. All samples were taken at random from the commercial catch except in 1952-53 when fishing was suspended because of a strike. In that year

TABLE IV. Annual age-composition weighted to 10,000 fish per year, and number of samples for the Lower East Coast Sub-district.

Year	Number of fish in year of age										Number of samples
	I	II	III	IV	V	VI	VII	VIII	IX	X	
1915-16	...	70	2213	3624	2613	1115	261	87	17	...	6
1916-17	...	20	4540	2065	2127	777	389	61	20	...	5
1917-18	...	16	3719	3850	930	1028	261	163	16	16	4
1918-19	...	44	5778	2022	1467	489	178	...	22	...	3
1919-20	...	26	1964	5788	1576	388	181	52	26	...	8
1921-22	4846	2712	1077	1000	231	135	10
1922-23	...	230	3305	4569	1264	259	287	57	29	...	7
1924-25	...	32	4511	3407	1230	694	95	32	3
1925-26	...	25	2594	5212	1571	175	399	25	6
1929-30	...	31	5109	2435	1920	480	25	10
1930-31	...	127	5222	3492	857	238	63	14
1931-32	...	271	4767	3091	1492	329	39	10	13
1932-33	...	110	3905	4541	1163	220	37	24	8
1933-34	...	201	6230	1879	1444	187	58	6
1934-35	...	50	4418	3786	819	731	140	55	8
1935-36	...	128	3995	3147	2047	132	422	97	32	...	3
1936-37	...	438	5274	2483	1169	444	109	82	17
1937-38	...	183	5233	2825	1231	398	130	11
1938-39	...	2556	3881	2372	778	284	69	55	...	6	14
1939-40	...	2318	5328	1225	699	280	127	12	9	3	21
1940-41	...	337	7736	1236	460	176	40	5	10	...	19
1941-42	...	272	3660	4774	991	194	68	29	12	...	41
1942-43	...	791	7478	1258	420	53	17
1943-44	5	1009	5496	2895	409	151	30	5	29
1944-45	42	2492	5654	1422	285	91	15	26
1945-46	14	787	7624	1413	129	22	11	58
1946-47	199	623	4807	3673	598	82	12	5	1	...	50
1947-48	48	179	4972	3380	1131	241	42	7	73
1948-49	6	277	7715	1763	196	43	31
1949-50	3	145	6608	2724	434	68	16	3	41
1950-51	3	421	6478	2388	565	118	20	6	1	...	64
1951-52	7	858	5843	2438	684	125	36	8	2	...	79
1952-53	14	228	5871	3478	340	57	7	3	100
1953-54	...	73	5841	3395	609	62	14	4	2	...	87

the samples were taken at random from the catch of a research vessel which used a seine of the same mesh but of smaller overall size than that of the commercial vessels.

The samples generally consisted of about 100 fish, except for those taken from 1915-16 to 1927-28, which varied in number from 25 to 250 fish. The number of samples per year, shown in Tables IV, VIII, IX and X, has depended on both the opportunity for sampling and the success of fishing. In recent years, particularly since 1940-41, sampling has been much more extensive than in earlier years and has averaged 51 per year (about 5,100 fish) for the lower east coast and 52 per year (about 5,200 fish) for the west coast. This is roughly equivalent to about one sample (100 fish) per 800 tons caught.

AGE ESTIMATION

Ages were estimated from the scales using methods described by Tester (1937, pp. 148-149). Roman numerals are used to designate the year of life of the fish. Thus III refers to a fish in its third year: if hatched in March and caught in November its exact age would be 2½ years.

Average annual age-compositions, weighted to 10,000 fish per year, are given in Tables IV, VIII, IX and X. Prior to 1933-34, when accurate individual area catches were not available, the age-composition for a year was obtained from the pooled data of all samples, regardless of the number of fish in each and where they were caught within the area embraced by the population. In 1933-34 and subsequent years, the age-composition for a year was obtained by averaging the percentage age-compositions of the samples from each area embraced by the population and then weighting the averages by the number of fish in the catches from each area before obtaining a grand average for each population. The data presented here have been published in part elsewhere either as histograms or in tables (e.g. Tester, 1936, 1937 and 1948), but not weighted to catch as just described.

SOURCES OF ERROR IN AGE-COMPOSITION

The purse seine catch is believed to be an unbiased or only slightly biased sample of the fishable stock. A few small fish may escape through the meshes of the seine during circling, pursing and initial fleeting operations, but with continued fleeting this is largely prevented by the fish massing against the web. If the schools are layered according to size with the smaller fish toward the top, as indicated by Thompson (1917, p. 47), selection might result if the larger and deeper individuals escaped capture. Usually the seines are not cast unless the fish are within about 15 fathoms of the surface. As the nets reach to about 40 fathoms, and frequently drag the bottom, it seems likely that the entire school is usually caught. Mesh size (1½ inches, stretched measure) has remained constant over the period. On the lower east coast of Vancouver Island there has been a change from double to single seining (Tester, 1935, pp. 10-12) which took place over the period 1938-39 to 1941-42. Although the actual mesh size of cutched 1½-inch web (double seines) is slightly larger than that of tarred 1½-inch web (single seines), it is doubtful if this would cause any noticeable difference in selection.

For the most part, the samples which have been examined were taken at random from the commercial catch. However, during the early years there may have been an unconscious rejection of the small fish of age I by the sampler when measuring the fish and, particularly, when taking the scale sample for age estimation (small fish readily lose their scales). This may account for the absence or infrequent occurrence of fish of age I in samples taken prior to 1943-44 (Tables IV, VIII, IX and X). This possible source of error would not affect the conclusions which have been drawn. It is unlikely that the sampler would unconsciously reject the larger fish of age II or older.

As the scales of herring from southern British Columbia often have faint annuli and pronounced secondary checks, doubtless some errors in age estimation have been made. Those collected from 1915-16 to 1925-26 were particularly difficult to interpret as the scale surfaces had become eroded from the formalin in which they had been preserved for several years before examination. Whether preserved or fresh, the scales of older fish are bothersome in herring as in other species because of the crowding of the annuli toward the edge. At the younger ages, errors in age-composition doubtless exist, also, but they tend to cancel out when the data are summarized. Consistency in interpretation is of prime importance, particularly when several different scale readers are involved. One person, the author, read all or most of the scales collected before about 1940-41. Since 1940-41 there have been several different readers, but every effort has been made to maintain consistency in interpretation; there has been very good agreement when trained readers have compared their estimations. It is believed that the readings are reasonably reliable and that the interpretations are reasonably consistent over the entire period.

RESULTS AND DISCUSSION: LOWER EAST COAST OF VANCOUVER ISLAND

Figure 2 shows that the catch in the lower east coast of Vancouver Island sub-district has generally increased over the 48-year period, but that large annual fluctuations have occurred. The fluctuations have been almost entirely the result of variable effort induced by changing economic conditions, and since 1936-37, changing catch quotas (Tester, 1945, p. 10). In the Figure, five periods of average high or low catch have been indicated by horizontal bars: (1) 1911-12 to 1914-15, (2) 1915-16 to 1921-22, (3) 1925-26 to 1931-32, (4) 1933-34 to 1938-39 and (5) 1942-43 to 1951-52. For convenience, the years of increasing catch between periods 4 and 5 have been designated period 4a. It might be noted that the low catch in 1952-53 was due to a labour strike and that the very high catch in 1953-54 resulted from quota extensions beyond 40,000 tons.

Although the catch fluctuates rather widely in all five periods except the last, it will be assumed to be stable within periods, and attempts will be made later to relate average referable catch and average mortality rates in order to estimate recruitment and natural mortality. First, however, the general nature of recruitment and mortality will be examined.

NATURE OF RECRUITMENT AND MORTALITY

When catch curves are plotted for individual years they are irregular or "bumpy" because of annual variation in recruitment and effort. One method of minimizing the variation is to average the data for several years. This has been done, arbitrarily, for seven successive five-year periods, i.e., 1915-16 to 1919-20, 1921-22 to 1925-26 (except 1923-24), 1929-30 to 1933-34, etc.

Average age-compositions are included in Table V and the resulting seven catch curves are plotted in Figure 3. The curves are labelled 1-2, 2, 2-3, 3-4, 4-4A, 4A-5 and 5 to indicate their relationship to the periods discussed above. An eighth curve, 5A, is for the combined data of the last two five-year periods, 1944-45 to 1953-54.

From the left-hand limb and dome of the curves it is evident that recruitment of a year-class to the fishable stock takes place mostly at age III, but that some members enter the fishery for the first time at ages I, II and IV. Whether recruitment extends beyond age IV is debatable. Curves 1-2 and 2-3, with domes extending to at least ages VI and V, respectively, suggest that recruits are entering at these advanced ages, although there are other possible explanations. Lack of fish at age I in the early years, together with a progressive sharpening of the dome at ages III and IV from curve to curve, suggests a progressive change in the nature of recruitment although, again, there are other explanations. It will be assumed for the present that recruitment takes place at ages I to IV only.

The right-hand limbs of the curves are based on data which become intrinsically less reliable with advancing age because of the smaller numbers included in the samples. Data for age IX are best ignored; those for age X have not been graphed. The right-hand limbs are in some cases convex, concave or sinuous and in others relatively straight. Curve 5A has a relatively straight right-hand limb, although this is the resultant of a slightly convex (upward) limb (curve 4A-5) and a slightly concave limb (curve 5). It might be assumed that curve 5A is roughly identifiable with period 5 and that the straight right-hand limb indicates a constant total mortality rate under equilibrium conditions. Although later it will be shown that a slightly convex right-hand limb seems to exist under equilibrium conditions, for the present it will be assumed to be

TABLE V. Average age-composition, weighted to 10,000 fish per annum, for successive five-year periods in the lower east coast sub-district.

Sampling years	Reference periods	Number of fish in year of age									
		I	II	III	IV	V	VI	VII	VIII	IX	X
1915-16 to 1919-20	1-2	...	35.2	3642.8	3469.8	1742.6	759.4	254.0	72.6	20.0	3.2
1921-22 to 1925-26 (except 1923-24)	2	...	71.8	3814.0	3975.0	1285.5	532.0	253.0	62.2	7.2	...
1929-30 to 1933-34	2-3	...	148.0	5046.6	3087.6	1375.2	290.8	44.4	6.8
1934-35 to 1938-39	3-4	...	671.0	4560.2	2922.6	1208.8	397.8	174.0	57.8	6.4	1.2
1939-40 to 1943-44	4-4A	1.0	945.4	5939.6	2277.6	595.8	170.8	53.0	10.2	6.2	0.6
1944-45 to 1948-49	4A-5	61.8	871.6	6154.4	2330.2	467.8	95.8	16.0	2.4	0.2	...
1949-50 to 1953-54	5	5.4	345.0	6128.2	2884.6	526.4	86.0	18.6	4.8	1.0	...
1944-45 to 1953-54	5A	33.6	608.3	6141.3	2607.4	497.1	90.9	17.3	3.6	0.6	...

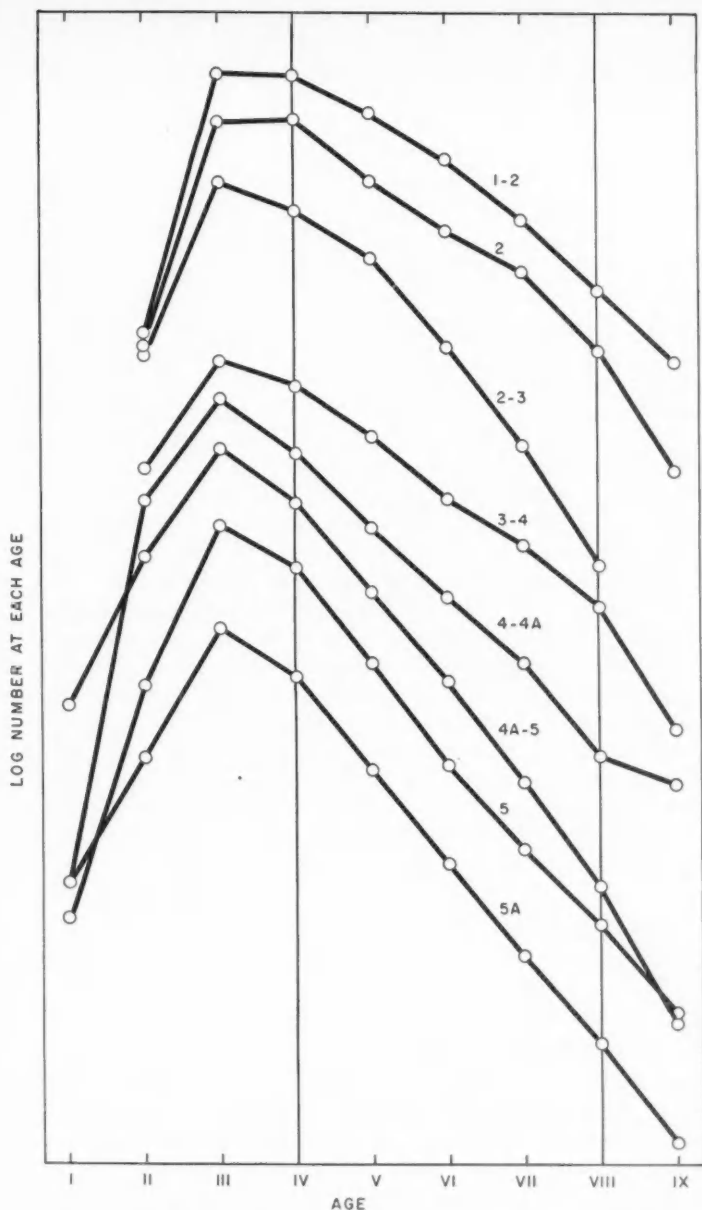


FIGURE 3. Average catch curves for successive five-year periods: 1-2, 1915-16 to 1919-20; 2, 1921-22 to 1925-26 (except 1923-24); 2-3, 1929-30 to 1933-34; 3-4, 1934-35 to 1938-39; 4-4A, 1939-40 to 1943-44; 4A-5, 1944-45 to 1948-49; and 5, 1949-50 to 1953-54. Curve 5A is based on ten years: 1944-45 to 1953-54.

linear in order to make rough calculations of the relative number of new recruits entering the fishable stock for the first time at ages I, II, III and IV.

By fitting a straight line to the logarithms of the age frequencies (Table V) from ages IV to IX, the slope of curve 5A is found to correspond with a total annual mortality rate (a) of 0.80 and a survival rate (s) of 0.20. Assuming a definitive survival rate of 0.20, 33.6 fish entering for the first time at age I (Table V) would decrease to 6.7 at age II. The new fish entering at age II would therefore number $608.3 - 6.7$ or 601.6. Continuing this process, the relative number of new fish entering for the first time at ages III and IV are respectively 6,019.6 and 1,379.1. On the basis of 10,000 recruits, the relative numbers entering the fishery for the first time at ages I to IV are respectively 42, 749, 7,493 and 1,717 (the numbers total 10,001 fish because of errors in rounding). These figures were used earlier to set up a mathematical model of the population. It might be noted that the relative numbers would change but slightly if allowance were made for a slight convexity of the right-hand limb such as might be induced by a progressive increase in natural mortality rate with age.

The above figures indicate the nature of recruitment of an average year-class during recent years. However, the data of Table IV show that it may differ considerably from year to year, apart from the possible trend in time already mentioned. Annual variation is well illustrated by the data of 1938-39, 1939-40, 1943-44 and 1944-45, when there were great influxes of fish at age II which cannot be adequately explained on the assumption that they all belonged to exceedingly rich year-classes. If so, they would have been expected to be dominant in the catches at ages greater than III in subsequent years. It is interesting to note that in the years of great influx of fish of age II the average lengths of the fish at this and older ages are relatively large, suggesting the hypothesis that in certain years abnormally rich feeding conditions produce accelerated growth, greater length and weight, earlier maturation and thus recruitment of a year-class at an earlier age:

Sampling years	Standard length (mm.) at ages				
	II	III	IV	V	VI
1929-30 to 1933-34	146.5	182.1	195.4	204.2	212.1
1938-39; 1939-40; } 1943-44; 1944-45 }	167.2	190.5	201.4	210.1	218.4
1949-50 to 1953-54	151.7	186.2	198.4	209.9	218.1

Curvature of the right-hand limb of the curves of Figure 3 could be due to several factors, the most obvious of which is a progressive change in effort, and thus in rate of fishing and catch, with time. Its effect may be reduced, if not eliminated, by averaging data which are referable only to periods of approximate stability. The portion of the data of Table IV pertaining to the right-hand limbs may be rearranged as in Table VI so that, reading horizontally, the numbers of fish at each age comparison are referable to the same pair of year-classes. The referable years and average referable catch for each year-class pair are also listed. At each age comparison, the numbers of fish in the year-class pairs were

TABLE VI. The data of Table IV (in part) arranged for comparison of pairs of adjacent year-classes at post-recruited ages, together with referable period, years, and catch in millions of fish.

Referable period	Number of fish in year of age								Referable years	Average referable catch
	IV	V	V	VI	VI	VII	VII	VIII		
1	261	87	1910-11; 1911-12	145
1	1115	261	389	61	1911-12; 1912-13	213
1	2613	1115	777	389	261	163	1912-13; 1913-14	227
1	3624	2613	2127	777	1028	261	178	...	1913-14; 1914-15	205.5
2	2065	2127	930	1028	489	178	181	52	1914-15; 1915-16	154.5
2	3850	930	1467	489	388	181	1915-16; 1916-17	142
2	2022	1467	1576	388	231	135	1916-17; 1917-18	146
2	5788	1576	1000	231	287	57	1917-18; 1918-19	135.5
2	1077	1000	259	287	1918-19; 1919-20	82
2	2712	1077	1264	259	95	32	1919-20; 1920-21	88.5
2	4569	1264	694	95	399	25	1920-21; 1921-22	166.5
	1230	694	175	399	1921-22; 1922-23	215.5
	3407	1230	1571	175	1922-23; 1923-24	191
	5212	1571	1923-24; 1924-25	158
	25	...	1924-25; 1925-26	258.5
3	480	25	63	...	1925-26; 1926-27	351.5
3	1920	480	238	63	39	10	1926-27; 1927-28	344.0
3	2435	1920	857	238	329	39	37	24	1927-28; 1928-29	385.5
3	3492	857	1492	329	220	37	58	...	1928-29; 1929-30	432
3	3001	1492	1163	220	187	58	140	55	1929-30; 1930-31	383
3	4541	1163	1444	187	731	140	422	97	1930-31; 1931-32	382.5
	1879	1444	819	731	132	422	109	82	1931-32; 1932-33	279
	3786	819	2047	132	444	109	130	...	1932-33; 1933-34	214
4	3147	2047	1169	444	398	130	69	55	1933-34; 1934-35	223.5
4	2483	1169	1231	398	284	69	127	12	1934-35; 1935-36	155
4	2825	1231	778	284	280	127	40	5	1935-36; 1936-37	195
4	2372	778	699	280	176	40	68	29	1936-37; 1937-38	248
4	1225	699	460	176	194	68	1937-38; 1938-39	263.5
	1236	460	991	194	53	...	30	5	1938-39; 1939-40	291.5
	4774	991	420	53	151	30	15	...	1939-40; 1940-41	307
	1258	420	409	151	91	15	11	...	1940-41; 1941-42	382
	2895	409	285	91	22	11	12	5	1941-42; 1942-43	464
5	1422	285	129	22	82	12	42	7	1942-43; 1943-44	437
5	1413	129	598	82	241	42	1943-44; 1944-45	396.5
5	3673	598	1131	241	43	...	16	3	1944-45; 1945-46	376.6
5	3380	1131	196	43	68	16	20	6	1945-46; 1946-47	353.5
5	1763	196	434	68	118	20	36	8	1946-47; 1947-48	336
5	2724	434	565	118	125	36	7	3	1947-48; 1948-49	370.5
5	2388	565	684	125	57	7	14	4	1948-49; 1949-50	389
5	2438	684	340	57	62	14	1949-50; 1950-51	376.5
5	3478	340	609	62	1950-51; 1951-52	362

summed for each period of approximately stable catch, and the average survival rate (s) and average instantaneous total mortality rate (i) were calculated. Thus, for ages IV to V in period 2, there are 18,941 fish at age IV and 6,314 fish at age V; $s = 6,314/18,941 = 0.3334$; $i = 1.098$. The average referable catch (C) is equal to $(142 + 146 + 135.5 + 88.5 + 166.5)/5$, or 135.7 million fish. The instantaneous total mortality rates and average referable catches are shown for all age comparisons and periods in Table VII.

Curvature of the right-hand limb may be visualized from the mortality rates of Table VII: a progressive increase in i indicates a convexity upwards, a progressive decrease indicates a concavity. As average referable catch (and presumably rate of fishing) is almost the same at each age comparison within

TABLE VII. Mortality rates (i) and average referable catches (C , in brackets) at successive age comparisons in periods 1 to 5 for the lower east coast sub-district.

Period	i and (C) at age comparisons			
	IV to V	V to VI	VI to VII	VII to VIII
1	0.327 (205.5)	0.918 (216.2)	1.165 (215.2)	1.253 (215.2)
2	1.098 (135.7)	0.925 (114.6)	1.081 (131.5)	1.402 (134.1)
3	0.908 (395.7)	1.554 (385.4)	1.797 (379.8)	1.406 (379.8)
4	0.710 (217.0)	1.008 (217.0)	1.121 (217.0)	1.102 (205.4)
5	1.659 (377.5)	1.745 (377.5)	1.699 (379.4)	1.471 (379.8)
Geometric mean of i	0.826	1.184	1.339	1.320

periods, curvature is probably due to some factor other than progressive change in rate of fishing. Apart from certain anomalies, there appears to be an increase in total mortality rate with increase in age, i.e. a convexity, in the data of periods 1 to 4. The anomalies are likely due to random variation in sampling or to failure to average out annual fluctuations in rate of fishing and recruitment. The data of period 5 appear to constitute a noteworthy exception, for they are based on much more extensive sampling than those of the earlier periods. However, if the middle five year-class pairs (Table VI) are averaged, yielding the same referable catch at all age comparisons (365.1 million fish), the mortality rates become 1.561, 1.621, 1.639 and 1.354. Only the last (calculated from ages VII to VIII) is low and this may be due to random variation, for the numbers of fish involved are small.

It is unlikely that a convexity of the right-hand limb would be produced by a progressive decrease in absolute recruitment (Ricker, 1948, p. 13). This would tend to change the slope of the limb without introducing much curvature. The convexity might be due to (1) a "reading down" of the ages of the older fish, perhaps combined with (2) recruitment extending to age V (or more), particularly in the early years. A more likely explanation (3) is that natural mortality rate increases progressively with increase in age. This may also be surmised from an analysis of the data of a newly exploited herring population, that of the Queen Charlotte Islands (Ricker, 1948, p. 30) in which there is a strongly convex right-hand limb. The convexity would be expected to be less pronounced under conditions of heavy exploitation when a large and constant rate of fishing is added to the changing natural mortality rate. In other little-exploited populations similar increases in mortality rate with age have been noted, e.g. in sauger, rock bass, and whitefish by Ricker (1949), and in lake trout by Kennedy (1954, p. 858).

In view of the anticipated change in natural mortality rate with age, it will be necessary to deal separately with each age comparison in the calculations of recruitment and natural mortality rate which follow.

ESTIMATE OF RECRUITMENT AND NATURAL MORTALITY RATE

If it is assumed that recruitment and natural mortality rate (at a given age) remain constant, they may be estimated at each age comparison for data pertaining to two or more periods of approximate stability from the equation relating i and C , determined earlier:

$$i = q + 1/R(iC)$$

Applying this relationship to data for periods 1 to 5 at the several age comparisons as derived from Table VII, the following least-squares solutions result:

$$\begin{array}{ll} i = 0.429 + 0.001887(iC) & \text{(IV to V)} \\ i = 0.688 + 0.001521(iC) & \text{(V to VI)} \\ i = 0.836 + 0.001367(iC) & \text{(VI to VII)} \\ i = 1.139 + 0.000529(iC) & \text{(VII to VIII)} \end{array}$$

There is an increase in apparent natural mortality rate (q) at successive age comparisons (0.429, 0.688, 0.836 and 1.139). The increase in the true rate would be expected to be somewhat greater than that indicated by the figures for, as pointed out earlier from the examination of a mathematical model, q tends to be slightly overestimated at ages IV to V, and slightly underestimated at ages VI to VII and ages VII to VIII. There is an increase in apparent recruitment (R) at successive age comparisons (530, 657, 732 and 1,890 million fish). This, also, was anticipated from the mathematical model. As already pointed out, the best estimate (still an overestimate) is, that at ages IV to V (530 million fish). It will be noted that the estimates of both q and R at ages VII to VIII appear to be too large. This is probably due to errors of sampling; the estimates become progressively less reliable toward the older age comparisons because of the decrease in numbers of fish on which the calculation of total mortality rate (i) is based. Although it is possible to calculate fiducial intervals for the estimates, this has not been done; their interpretation would be questionable because the variates are average ratios of varying intrinsic accuracy. However, the relatively small variance from regression may be judged from the scatter of the points about the line of best fit as shown in Figure 4.

Better estimates of q and R might be expected from the data of periods 4 and 5, when sampling was generally more extensive and the measure of catch more reliable than in the earlier periods. Using average values of i and iC derived from Table VII for these two periods only, the estimates of q at the several age comparisons become 0.400, 0.642, 0.771 and 0.851, and the estimates of R become 498, 597, 694 and 901 million fish. The apparent natural mortality rates are slightly less than those calculated from the data of all five periods, but they increase more regularly. The best estimate of R , 498 million fish, is also less.

Investigation of the mathematical model indicated the possibility of obtaining approximately accurate estimates of R and q when effort (and thus catch) is

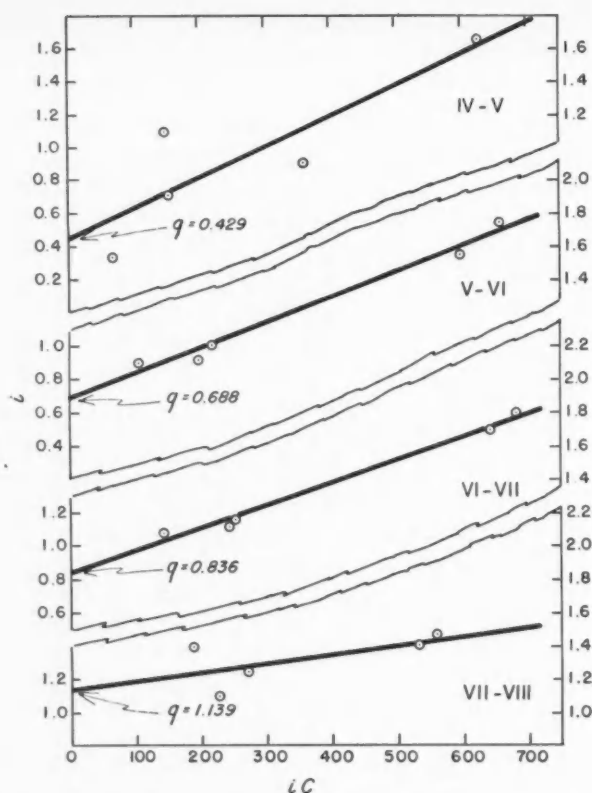


FIGURE 4. Relationship between instantaneous total mortality rate (i) and the product of mortality rate and average referable catch (iC) at each of four age comparisons (IV to V, V to VI, VI to VII and VII to VIII) for data of periods 1 to 5, inclusive. The value of instantaneous natural mortality rate (q) is indicated in each graph.

changing, providing there is no overall trend during the period under consideration. Application of the equation to data for individual year-class comparisons from periods 3 to 5 (Table VI) yields estimates of q at ages IV to V and V to VI of the same order of magnitude as those given above (0.345 and 0.534, respectively). However, at ages VI to VII and VII to VIII the estimates (0.560 and 0.301) are low because of the necessary omission of data for the large number of comparisons in which no fish occur in the older age-group (i is infinitely large). This difficulty does not occur when the data of several year-classes are summed before calculating i , as was done in compiling the data of Table VII.

It is difficult to escape the conclusion that in the herring population under consideration, natural mortality rate is not only high among post-recruited groups but also increases progressively with age. The instantaneous natural

mortality rates (q) estimated at ages IV to V, V to VI, VI to VII and VII to VIII from the data of periods 4 and 5 (0.400, 0.642, 0.771 and 0.851) correspond with annual rates (n) of 33, 47, 54 and 57 per cent. The annual rates are generally higher than are those estimated for other species of marine fish which support major fisheries, e.g. 5 to 20 per cent for the North Sea cod (Graham, 1935, p. 268), 25 per cent for the Skagerrak plaice (Baranoff, 1918, p. 13), 30 per cent for the North Pacific halibut south of Cape Spencer (Thompson and Herrington, 1930, p. 71), and 13 per cent for the Pacific pilchard (Silliman, 1943, p. 6). However, the average rate (about 48 per cent) is similar to that (50 per cent) used by Tester (1948, p. 157) in considering the efficacy of catch quotas in regulating the British Columbia herring fishery.

It is realized that the above estimates of absolute recruitment and natural mortality rate for the lower east coast of Vancouver Island herring population are subject to large and unknown errors. As more reliable estimates from other sources (age-composition and effort; tagging) are not available, they will be accepted for the present and used to calculate other statistics of the population during the recent period of approximately stable catch.

ESTIMATE OF ABUNDANCE OF THE FISHABLE STOCK

Although the estimate of absolute recruitment given in the preceding section forms a good basis for comparing the magnitude of herring stocks in different areas, it is worth while to estimate the average abundance of the fishable stock at the start of the fishing season in period 5 in order that it may be compared with a similar estimate obtained from other data.

If natural mortality rate remains constant over all age-groups, average initial abundance of the fishable stock (N) during a period of equilibrium may be estimated readily from knowledge of instantaneous natural mortality rate (q), instantaneous total mortality rate (i) and average catch (C). These statistics lead to estimates of instantaneous rate of fishing ($p = i - q$), annual total mortality rate ($a = 1 - e^{-i}$), rate of exploitation ($u = pa/i$) and, finally, initial population number ($N = C/u$). If natural mortality rate increases with age, as seems to be the case in the herring population, the foregoing calculations must be repeated at each age, and successive values of $N_1, N_2 \dots N_n$ must be summed to give N .

Graphic extrapolation of the natural mortality rates given in the preceding section (with due allowance for over- and underestimations as discussed previously) yields the following estimates at the several age comparisons from ages I to II to ages IX to X, inclusive: $q = 0.12, 0.25, 0.38, 0.51, 0.64, 0.77, 0.90, 1.03$ and 1.16 . Although there are large potential errors in the extrapolated values, they will not greatly affect the magnitude of summation N , as it is determined largely by the rates which are more accurately estimated near the centre of the age range. The best estimate of p is that for ages V to VI when q is most accurately estimated (0.64). Given $i = 1.74$ (Table VII), $p = 1.74 - 0.64 = 1.10$. Assuming p to be constant at the various ages, it may be combined with each q to provide estimates of i and a and thus the following estimates of u to be applied

to each age: I-0.636, II-0.604, III-0.571, IV-0.547, V-0.521, VI-0.498, VII-0.476, VIII-0.455 and IX-0.436. Given an average catch for period 5 of 377.5 million fish, this may be distributed according to average age-composition as follows: I-1.23, II-28.62, III-236.60, IV-88.16, V-18.31, VI-3.75, VII-0.69, VIII-0.13, IX-0.01 million fish. Dividing C by u at each age and summing, $N = 667$ million fish (71 thousand tons).

Stevenson and Outram (1953, pp. 71-75) estimated the fishable stock in the same area, the lower east coast of Vancouver Island sub-district, by adding the number of fish in the catch to the number in the spawning population, estimating the latter from the number of miles of spawn deposited after the close of the fishing season and the number of eggs and equivalent number of spawning fish per unit area. Their estimates for the years 1946-47 to 1951-52 are respectively 484, 525, 700, 596, 597 and 740 million fish, yielding an average of 607 million fish. While this is smaller than that given above (667 million fish) it is of the same order of magnitude. Their estimates would have been increased had it been possible to allow for natural mortality from the start of the fishing season to the end of the spawning season (5 months). The similarity of the two estimates is either a remarkable coincidence, or it indicates the general reliability of both of the rough methods which have been used.

RESULTS AND DISCUSSION: WEST COAST OF VANCOUVER ISLAND

As shown in Figure 5 (Tables VIII, IX and X), the catch for the three west coast of Vancouver Island populations has fluctuated considerably over the 25-year period under consideration (1929-30 to 1953-54), particularly in Area 25-26 and Area 27. It is difficult to select any periods of approximate catch stability similar to those for the lower east coast fishery. The fluctuations have been due partly to changes in effort induced by changing economic conditions and government regulations, and partly to changes in the availability and abundance of the fishable stocks (Tester, 1948, pp. 136-142). Since 1945-46 there have been no quota restrictions on fishing; in 1952-53 there was no commercial fishery because of a strike.

To obtain preliminary information on the nature of recruitment and mortality, the age-compositions for Area 23-24 (Table VIII) and Area 25-26 (Table IX) were averaged separately over the 25-year period and plotted as catch curves in Figure 6. From the left-hand limbs it is obvious that recruitment takes place at age I and II but reaches a maximum at age III. Presumably, as in the lower east coast population, recruitment also takes place at age IV and perhaps at older ages, but this cannot be ascertained with certainty because of the general convexity of the right-hand limbs. It is unlikely that the convexity is caused by a progressive decrease in rate of fishing over the period: catch, and presumably rate of fishing, has tended to increase slightly rather than to decrease. It seems more likely that the convexity is associated with an increase in natural mortality rate with advancing age.

The data of Area 27 are of particular interest in this regard. The area was not fished until 1929-30 and was exploited to but a small extent from that year

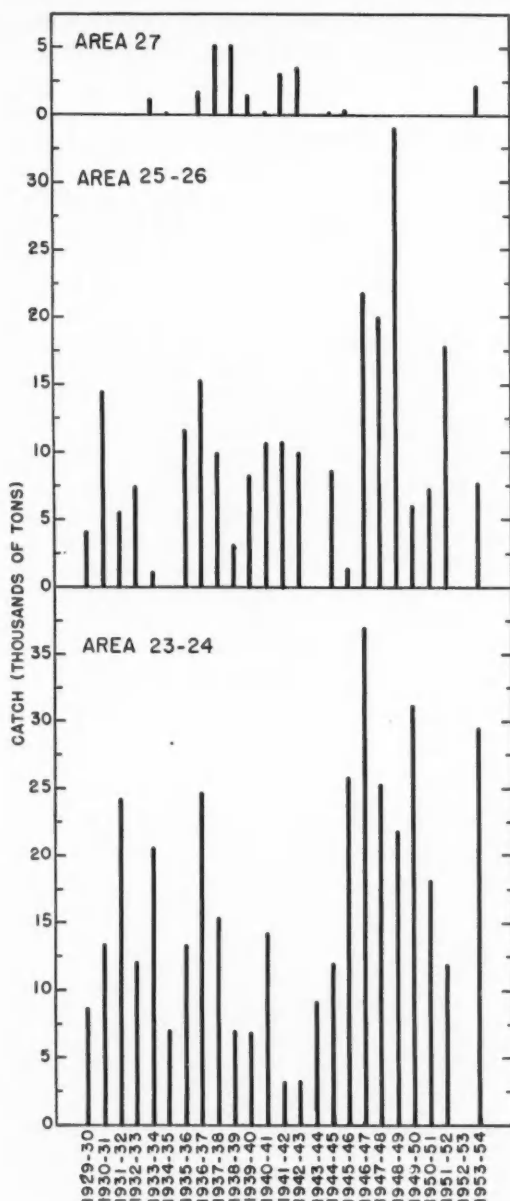


FIGURE 5. Catch of herring in Areas 23-24, 25-26 and 27 of the west coast of Vancouver Island sub-district.

until 1937-38. The average catch curve for the years 1932-33 to 1937-38, included in Figure 6, should reflect near-virgin conditions in the stock. Both because of excessive random variation associated with inadequate sampling and because of large annual variation in recruitment, the average curve is irregular. A smooth curve drawn by eye through the plotted points shows a flattened dome merging into a convex right-hand limb. From the smooth curve the following total mortality rates, which may be assumed to approximate natural mortality rates (q), may be calculated at successive age comparisons: IV to V-0.32, V to VI-0.47, VI to VII-0.73 and VII to VIII-1.17. Assuming recruitment is completed at age IV, an increase in natural mortality rate at successive ages is again indicated.

To obtain rough approximations to R and q , the age-composition and catch data for Areas 23-34 and 25-26 were arranged as in Table VI for the lower east coast of Vancouver Island (the tables are not included here, but may be constructed from the data of Tables VIII and IX) and apparent instantaneous mortality rates (i) and average referable catches (C) were calculated for each pair of year-classes at each age comparison. The equations of the lines of best fit between i and iC were determined by least squares, without attempting to select periods of stable catch, yielding estimates of R and q which are given in Table XI. The calculations were repeated for the combined data of Area 23-24

TABLE VIII. Annual age-composition weighted to 10,000 fish per year, number of samples, and catch in weight (thousands of tons) and number (millions of fish) for Area 23-24 of the west coast sub-district.

Year	Number of fish in year of age										No. of samples	Catch	
	I	II	III	IV	V	VI	VII	VIII	IX	XI		Weight	No.
1929-30	36	121	6741	1957	617	470	47	11	20	8.5	74.09*
1930-31	...	479	5622	3476	379	44	5	13.5	117.68*
1931-32	...	85	3210	3603	2995	108	16	24.2	210.95
1932-33	...	150	3939	2761	1977	1142	15	...	15	...	11	12.1	114.95
1933-34	...	254	6006	2051	796	679	215	10	20.6	187.26
1934-35	...	196	4607	4265	551	252	118	11	7	7.0	66.22
1935-36	...	264	6602	1670	1310	126	14	14	7	13.3	127.49
1936-37	7	591	5558	2808	624	383	19	...	10	...	10	24.6	256.48
1937-38	...	696	6020	1832	1090	181	117	39	14	13	8	15.3	156.95
1938-39	...	5237	3080	1336	199	129	20	12	7.0	79.97
1939-40	...	1818	5916	1536	552	103	66	...	8	...	11	6.9	62.09
1940-41	...	366	4349	3697	1196	321	46	19	6	...	16	14.3	122.36
1941-42	...	191	4011	2435	2528	643	133	49	10	...	8	3.4	30.11
1942-43	...	625	1913	4162	2314	715	202	69	9	3.5	27.70
1943-44	...	1135	4400	1705	1860	751	131	14	4	...	19	9.1	79.28
1944-45	604	3400	3971	1242	268	371	124	9	11	...	29	12.0	124.44
1945-46	...	1123	7495	982	239	54	90	14	2	...	43	25.9	244.75
1946-47	1	601	5194	3406	567	183	32	10	5	...	58	37.0	354.61
1947-48	5	356	6154	2504	799	146	21	13	2	...	61	25.3	239.05
1948-49	13	1495	5435	2558	362	107	26	4	24	21.8	226.41
1949-50	5	452	6756	2150	541	68	21	6	67	31.2	282.50
1950-51	5	1271	3823	4091	646	134	26	2	2	...	40	18.2	168.19
1951-52	5	522	6574	2005	794	81	18	17	11.9	111.90
1952-53	7	889	5567	3285	194	54	4	26
1953-54	9	270	6429	2664	544	59	15	6	3	...	63	29.5	291.83

*Estimated.

TABLE IX. Annual age-composition weighted to 10,000 fish per year, number of samples, and catch in weight (thousands of tons) and number (millions of fish) for Area 25-26 of the west coast sub-district.

Year	Number of fish in year of age											No. of samples	Catch	
	I	II	III	IV	V	VI	VII	VIII	IX	X	XI		Weight	No.
1929-30	3.8	35.22 ^a
1930-31	...	70	5594	4056	280	1	14.5	134.40 ^a
1931-32	...	110	4015	3774	2093	8	8	5.5	50.98
1932-33	...	109	4170	3589	1500	611	6	15	9	7.4	72.52
1933-34	...	209	7624	1358	705	78	26	5	1.1	11.72
1934-35
1935-36	7917	2083	1	11.5	116.18
1936-37	...	734	3280	4907	753	247	29	27	17	6	...	9	15.3	141.87
1937-38	...	134	6022	1363	1982	331	120	19	20	9	...	14	9.9	90.09
1938-39	...	1708	4594	3262	203	209	24	4	3.0	26.10
1939-40	2	5360	2851	1032	661	59	23	11	16	8.1	84.38
1940-41	...	302	8028	1074	373	181	28	14	21	10.7	97.83
1941-42	...	252	5927	3321	369	90	42	5	10.7	110.45
1942-43	...	457	2332	3982	2505	544	145	36	9	9.8	80.57
1943-44
1944-45	...	1224	2616	2517	1595	1475	535	27	11	9	8.3	62.83
1945-46	...	795	5499	1322	1192	884	268	40	4	1.4	12.33
1946-47	4	300	5507	2835	652	376	196	112	8	8	...	25	22.0	190.32
1947-48	...	87	5359	3151	924	303	101	46	25	2	2	56	19.9	173.76
1948-49	...	112	3749	3903	1461	535	166	58	14	3	...	39	34.1	276.27
1949-50	...	370	7471	1560	450	136	9	3	14	6.1	57.29
1950-51	...	154	2699	5463	1223	359	103	2	7.0	60.21
1951-52	...	19	1011	2723	5254	732	212	42	5	37	18.1	127.20
1952-53	27	2278	6058	1456	135	40	7	15
1953-54	4421	4262	939	275	104	5	7.7	74.15

^aEstimated.

TABLE X. Annual age-composition weighted to 10,000 fish per year, number of samples, and catch in weight (thousands of tons) and number (millions of fish) for Area 27 of the west coast sub-district.

Year	Number of fish in year of age											No. of samples	Catch	
	I	II	III	IV	V	VI	VII	VIII	IX	X	XI		Weight	No.
1932-33	424	2415	2797	3941	85	254	85	1	+	0.40 ^a
1933-34	3895	974	1947	1901	1129	154	2	1.2	11.30
1934-35	...	42	4884	2404	387	732	689	862	2	0.2	1.88 ^a
1935-36	4175	2330	2913	291	291	1	+	0.40 ^a
1936-37	...	48	1438	5627	959	1591	290	48	2	1.7	15.17
1937-38	...	248	3913	2014	2458	746	472	49	50	25	25	4	5.1	47.02
1938-39	...	851	782	4947	1181	1535	267	303	89	16	29	8	5.1	36.54
1939-40	...	926	3518	926	3426	556	370	92	185	1	1.5	12.29
1940-41	0.1	0.82 ^a
1941-42	...	392	5490	3431	196	1	3.0	31.27
1942-43	...	169	2305	3256	3396	699	120	55	4	3.5	29.42
1943-44	+	0.40 ^a
1944-45	...	526	2105	5368	1053	731	210	1	0.1	0.94
1953-54	4742	4036	1021	79	121	3	2.1	20.51

^aEstimated.

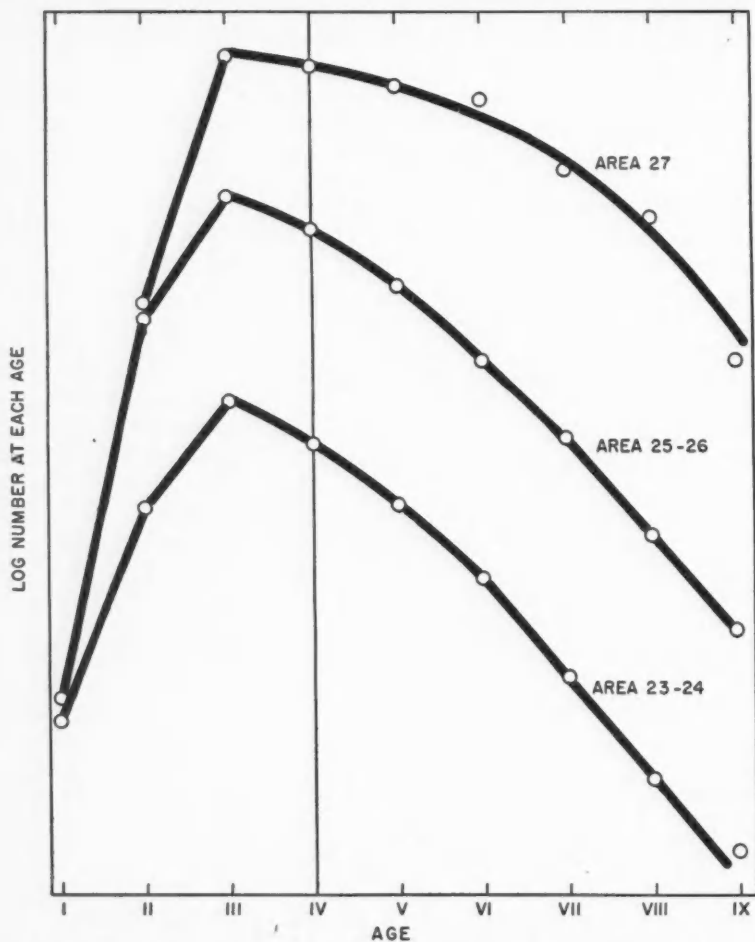


FIGURE 6. Average catch curves for areas of the west coast of Vancouver Island sub-district, based on data for the following years: Area 23-24, 1929-30 to 1953-54; Area 25-26, 1930-31 to 1953-54; Area 27, 1932-33 to 1937-38.

TABLE XI. Estimates of recruitment (R) and instantaneous natural mortality rate (q) at four age comparisons for areas of the west coast sub-district.

Age comparison	Area 23-24		Area 25-26		Area 23-26		Area 27
	R	q	R	q	R	q	q
IV to V	282	0.481	143	0.310	411	0.448	0.324
V to VI	315	0.580	204	0.609	325	0.609	0.467
VI to VII	307	0.671	294	0.933	540	0.720	0.728
VII to VIII	370	0.901	161	0.597	498	0.792	1.174

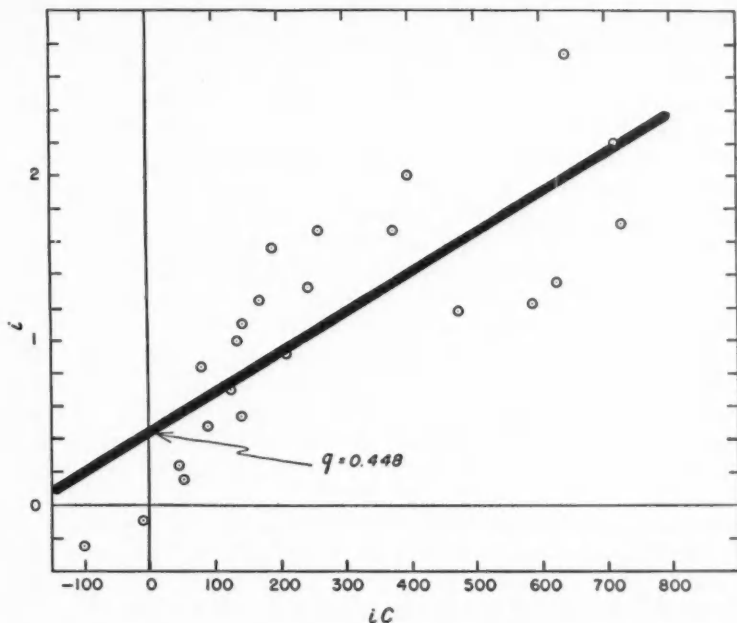


FIGURE 7. Relationship between instantaneous total mortality rate (i) and the product of mortality rate and average referable catch (iC) at ages IV to V for Area 23-26 of the west coast of Vancouver Island sub-district. The value of instantaneous natural mortality rate (q) is shown.

and Area 25-26, designated as Area 23-26. Table XI also includes the estimates of q for Area 27 as derived above from the catch curve.

It was pointed out previously that the best estimate of average absolute recruitment, still maximal, is that from the youngest age comparison. Thus R is estimated at 282 million fish for Area 23-24 and 143 million fish for Area 25-26, yielding a total of 425 million fish for both. This is similar in magnitude to the estimate of 411 million fish from the combined data (Area 23-26).

In both Area 23-24 and Area 24-25, the instantaneous natural mortality rate (q) appears to increase with age. A low value for Area 25-26 at age VII to VIII is doubtless caused by loss of data from year-class comparisons in which no fish were sampled at age VIII. In general the estimates agree with those obtained for Area 27, discussed previously, and also with those for the lower east coast of Vancouver Island, which were given in a previous section.

The variability of the points about the fitted line is shown for data pertaining to ages IV to V, Area 23-26, in Figure 7. This will be referred to in an appendix to this report.

SUMMARY AND CONCLUSIONS

A study has been made of age-composition and catch data collected over a long period of years from the purse seine herring fisheries of the lower east and west coasts of Vancouver Island to obtain basic information on recruitment and mortality.

Unfortunately effort is not necessarily proportional to rate of fishing, thus eliminating methods devised by others for estimating natural mortality rate. However, a relationship has been established between total mortality rate (i) and catch (C) which permits the calculation of absolute recruitment (R) and natural mortality rate (q) from age-composition and catch data for two or more periods of equilibrium, assuming the same absolute recruitment and the same natural mortality rate in each: $i = q + (1/R)iC$.

Average i may be determined from age-composition and average C from catch with allowance for a time lag in the relationship. However, when fluctuations in rate of fishing occur, more accurate estimates of R and q may be obtained by calculating "average referable catch", the average of the catch in years x and $x + 1$, and relating it to apparent i determined at ages IV to V in year $x + 2$, V to VI in year $x + 3$, etc. This approximation applies only to a population in which recruitment is presumed to spread over ages I to IV in a certain ratio. The ratio is such that, at age IV the survivors from recruitment at ages I and II are negligible, whereas the survivors from recruitment at age III are approximately equal to the recruits at age IV.

When q increases with advancing age, R is progressively overestimated at successive age comparisons and is best estimated from data at ages IV to V; q is overestimated at ages IV and V and underestimated at ages VI to VII and VII to VIII. No correction can be made for annual fluctuations in recruitment other than to average data for a number of years and to assume that their effect on apparent total mortality rate and catch will average out.

Average catch curves are used to study the nature of recruitment and mortality in the lower east and west coast of Vancouver Island populations. Recruitment of a year-class takes place mostly at age III but is spread from age I to at least age IV. Whether it extends to older ages is debatable.

The ratio at which recruits of a year-class are added to the fishable stock varies greatly from year to year, but has averaged 42 : 749 : 7,493 : 1,717 over a recent ten-year period for the lower east coast of Vancouver Island. A convexity in the right-hand limb of catch curves for periods of approximately stable catch indicates that natural mortality rate increases with age.

From data for five periods of approximate stability in the lower east coast of Vancouver Island fishery, R is calculated at 530 million fish (slightly overestimated), and q is calculated at 0.429, 0.688, 0.836 and 1.139 at ages IV to V, V to VI, VI to VII and VII to VIII, respectively (the first is slightly overestimated; the last two are slightly underestimated). From more reliable data for two recent periods of approximate stability, R becomes 498 million fish and q becomes 0.400, 0.642, 0.771 and 0.851 at the several age comparisons.

By extrapolating the estimates of natural mortality rate to other age-groups and using estimates of total mortality rate and average referable catch during a recent period of approximate stability, average initial abundance of the fishable stock is calculated at 667 million fish (71,000 tons) for the lower east of Vancouver Island population. This figure agrees closely with that obtained by adding spawning stock, as estimated from egg deposition and other data, to catch.

A convexity in the right-hand limb of the average catch curves for Areas 23-24 and 25-26 indicates that natural mortality rate also increases with advancing age in the west coast of Vancouver Island populations. This conclusion is strengthened by a pronounced convexity in the curve for Area 27, which reflects conditions in an almost unexploited population.

Using the formula given above and west coast of Vancouver Island data pertaining to all years rather than only to periods of equilibrium, estimates of R and q are obtained for the populations of Area 23-24 and Area 25-26, both individually and in combination (Table XI). For the combined data, R is estimated at 411 million fish, or slightly less than that for the lower east coast of Vancouver Island (498 million fish). For the combined data, q is estimated at 0.448, 0.609, 0.720 and 0.792 for the successive age comparisons. These estimates are similar in magnitude to those for the lower east coast of Vancouver Island.

Finally it should be emphasized that the estimates of average annual recruitment and average natural mortality rate are admittedly rough approximations with unknown fiducial limits. However it seems safe to conclude (a) that the estimates are at least of the correct order of magnitude, and (b) that natural mortality rate increases with age in British Columbia herring populations.

APPENDIX: USE OF AGE COMPOSITION AND EFFORT DATA TO ESTIMATE NATURAL MORTALITY RATE IN HERRING POPULATIONS

Beverton (1954) has shown that a straight line relationship exists between total instantaneous mortality rate ($F + M$) and fishing intensity or effort ($f = E$) which enables instantaneous natural mortality rate (M) to be estimated as the intercept on the ($F + M$) axis when $E = 0$. The equation, which is applicable to data for two or more periods of stability, may be written as follows, using Ricker's symbols for mortality rates:

$$i = q + cE$$

where c , the slope of the line, is the "catchability" or fraction of the stock taken by one unit of effort. When rate of fishing is changing, the above equation may be used as a first approximation in estimating q , but a method of iteration is required to obtain a more accurate estimate from the relationship which will now apply:

$$i_1' + \log_e \left(\frac{i_1 a_2}{i_2 a_1} \right) = q + cE_1$$

where i'_1 is the apparent instantaneous mortality rate in year I derived from the number of fish present at age n in year I and $n + 1$ in year 2. This method of estimating q was applied to herring data.

Effort (total number of seine-days) and catch per unit of effort (average catch per seine per day) for the lower east coast of Vancouver Island fishery are included in Table XII for double seines over the period 1933-34 to 1941-42 and for single seines over the period 1938-39 to 1951-52. The two types of gear and methods of fishing are described by Tester (1935, pp. 10-12). The data must be considered separately as the gear differs in efficiency.

TABLE XII. Effort (E), catch per unit of effort (C/E), adjusted number of fish at ages V (in year x) and VI (in year $x + 1$), and instantaneous total mortality rate (i') for (A) single seines and (B) double seines in the lower east coast of Vancouver Island sub-district.

Year x	A					B				
	E	C/E	V	VI	i'	E	C/E	V	VI	i'
1933-34	340	28.2	1197	799	0.404
1934-35	153	109.3	895	140	1.856
1935-36	162	105.8	2166	405	1.677
1936-37	271	91.3	1067	573	0.622
1937-38	174	144.0	1773	275	1.864
1938-39	271	96.9	754	234	1.170	506	52.0	405	96	1.440
1939-40	387	83.5	584	176	1.199	1059	34.2	239	94	0.934
1940-41	324	100.1	460	146	1.148	1674	53.4	246	190	0.259
1941-42	651	75.3	499	98.0	971	46	3.058
1942-43	510	86.0	361	60	1.796
1943-44	1065	39.8	163	27	1.796
1944-45	1339	29.5	84	9	2.235
1945-46	950	42.1	54	32	0.523
1946-47	929	39.3	235	159	0.390
1947-48	605	66.0	746	58	2.551
1948-49	296	135.6	266	65	1.411
1949-50	424	95.0	412	129	1.162
1950-51	375	109.2	617	84	1.995
1951-52	613	66.9

Age-composition data of Table IV were weighted to catch per unit of effort in an attempt to correct for fluctuations in recruitment. From the adjusted age-composition data, apparent mortality rates (i') were calculated at ages V (year x) to VI (year $x + 1$) for the same year-class (Table XII). A straight-line relationship between i' and E (first iteration) was obtained by the method of least squares for data pertaining to (A) double and (B) single seines:

$$(A) i' = 2.14 - 0.00448 E$$

$$(B) i' = 2.19 - 0.00087 E$$

In both equations, the slope (c) is negative. Obviously this is incorrect; it violates the basic assumption that rate of fishing ($p = i - q$) increases proportionately with effort ($p = cE$). This invalidates the estimates of q .

The assumption that rate of fishing is proportional to effort is strictly applicable only when the population is randomly distributed in space and time, and there is no competition between gear. The lower east coast fishery operates on temporary accumulations of an immigrating population. If the runs are late,

or if fishing starts early, considerable effort will be wasted in "scratch" fishing and competition between gear will be keen. If the run is early, or if fishing starts later than usual, there is no comparable waste of effort. Instead, there is often a conservation of effort by pooling resources: if a boat cannot handle a large "set", it is assisted by other boats which share the catch. Moreover, there is no assurance that the fraction of the total population which enters the fishery during the short fishing season is consistent from year to year. In fact, there is evidence to the contrary. In some years in which relatively poor fishing is encountered towards the close of the season, large quantities of fish may arrive just prior to the spawning season (February and March) to produce better than average egg depositions. Finally it might be noted that the efficiency of fishing, and thus the catchability (c) has doubtless increased throughout the years with an increase in packer and plant capacity and with the introduction of the radio telephone and echo sounder (Tester, 1945, pp. 15-17).

Beverton (1954, p. 121) applied the above method of estimating q to effort and age-composition data published by Tester (1948, Tables II and VI) for the west coast of Vancouver Island (Areas 23 to 27) over the period 1933-34 to 1944-45. He also found that the slope (c) of the line relating i and E was negative. However he wrongly interpreted the published age data, confusing those for the same year-class (proceeding horizontally in the table) with those for successive year-classes (proceeding diagonally). The data, correctly arranged, are given in Table XIII. Applying the equations, a first iteration yields a natural mortality rate (q) of 0.886 ($c = 0.000085$); a second iteration decreases it to 0.800 ($c = 0.000161$). The variation of the points about the fitted line (first iteration) is shown in Figure 8.

Although the slope of the line is positive, the variation of the points is so great that the addition or omission of one or two might readily change the slope from positive to negative. The variation is greater than that about the straight line relating i and iC (Fig. 7), giving more confidence in the former estimate of q (0.448), which was based on the same age comparison (IV to V) but used

TABLE XIII. Effort (E), adjusted number of fish at Ages IV (in year x) and V (in year $x + 1$), and instantaneous total mortality rate (i') for the west coast sub-district.

Year x	E	Number at age		i'
		IV	V	
1933-34	519	82	32	0.939
1934-35	119	232	84	1.015
1935-36	365	108	33	1.186
1936-37	818	178	53	1.211
1937-38	858	55	10	1.704
1938-39	848	53	18	1.078
1939-40	907	25	19	0.279
1940-41	1028	59	14	1.437
1941-42	814	63	59	0.067
1942-43	620	89	28	1.156
1943-44	550	26	28	-0.074
1944-45	592	62	16	1.356

catch rather than effort data. Again, as for the lower east coast fishery, effort is not necessarily proportional to rate of fishing nor is catch per unit of effort necessarily proportional to average abundance of the fishable stock, thus invalidating the estimate of q based on Beverton's method.

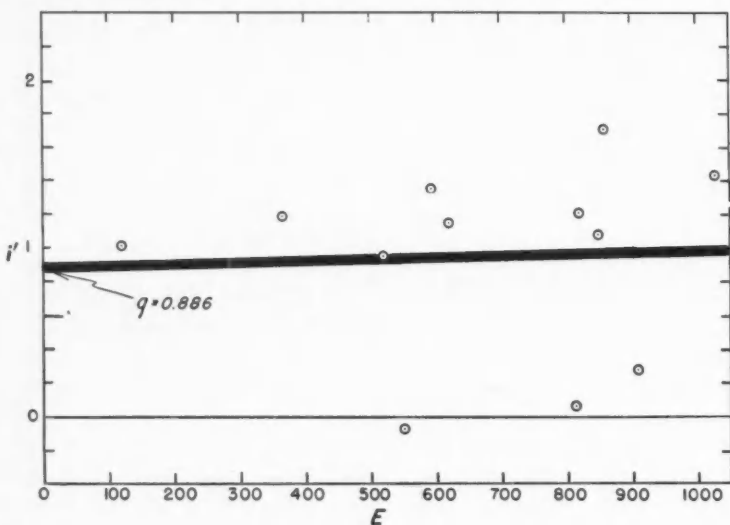


FIGURE 8. Relationship between instantaneous total mortality rate (i') and effort (E) at ages IV to V for Area 23-27 of the west coast of Vancouver Island sub-district. The value of instantaneous natural mortality rate (q) is shown.

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Pollution Survey of Humber Arm and Exploits River¹

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ABSTRACT

In 1942 a pollution survey was made of Humber Arm, Bay of Islands, and Exploits River, Notre Dame Bay, Newfoundland, where pulp and paper mills are situated.

Fresh water from the Humber River affects the salinity of the water in Humber Arm mainly to a depth of about 10 metres. The salinities and sulphates increased from the surface to the bottom while the temperature and dissolved oxygen decreased. No sulphite was detected. It was concluded that the operations of the mill have no injurious effects on fish life in Humber Arm.

On the Exploits River the dissolved oxygen was decreased by the mill effluents, and sulphite was detected in appreciable quantities, but neither of these effects was sufficient to harm fish life.

INTRODUCTION

THERE are two pulp and paper mills in Newfoundland, Bowater's Newfoundland Pulp and Paper Mills, Ltd., at Corner Brook on Humber Arm, Bay of Islands, and the Anglo-Newfoundland Development Co., Ltd., at Grand Falls on the Exploits River which empties into Notre Dame Bay. Salmon (*Salmo salar*) frequent both bodies of water where salmon angling and commercial fisheries are important, especially in the Humber area. The investigation was undertaken in 1942 in order to ascertain whether or not the waste products of these paper mills were polluting the waters to any appreciable extent.

In the production of newsprint and sulphite pulp in Newfoundland wood chips are cooked with sulphur dioxide, generally as calcium bisulphite, superheated steam being passed through the mixture for several hours. The cellulose fibres are thus separated when the lignin dissolves. After the cooking most of the calcium bisulphite is drained off to be used again, and the remaining mixture is washed thoroughly with water. The washing water is discharged by sewer into the nearest available natural waters. At Corner Brook the amount of free and combined sulphur dioxide in the sewer was 0.64 per cent while at Grand Falls it was 0.0027 per cent. The companies do not have records of volume of effluent discharged, but they kindly provided information on the rate of pulp production at the time of the investigation. At the Corner Brook mill the average daily production of sulphite pulp was 232 air-dry tons (210 metric tons) for the year 1942 and 235 tons (213 m.t.) for the month of August, 1942, when the survey was made. At the Grand Falls mill the average daily production of sulphite pulp was 125 bone-dry tons (113 m.t.) for the year 1942 and waste

¹Received for publication February 15, 1955.

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liquor was reported to be approximately 2,000 gallons (9.1 kl.) to the ton (0.9 m.t.).

No complete analysis of the waste sulphite liquor was available either at Corner Brook or Grand Falls. While the composition may vary with locality and mill, the components are the same. It is mainly a mixture of the calcium salts of sulphuric and sulphurous acids, lignones, sulphones, sulphonates, sugars and tannins. The liquor also contains small quantities of formic acid, acetic acid, methyl and ethyl alcohols, acetone and furfural (Benson, 1937).

These constituents of the waste-sulphite liquor have the following effects on natural waters which may be harmful to aquatic life: (1) they reduce the dissolved oxygen content, (2) they give the water a high acidity, and, (3) they are directly toxic themselves and/or may produce toxic products upon subsequent reaction in the water. The waste-sulphite liquor reduces the dissolved oxygen in the water in two ways. The organic constituents such as sugars and lignins oxidize to yield carbon dioxide and water. The inorganic constituents also oxidize, e.g. sulphites oxidize to sulphates. These reactions reduce the amount of dissolved oxygen available for aquatic life. If enough of it is used up, the aquatic life will be destroyed.

Nightingale and Loosanoff (1928) concluded that the sulphite liquor concentration could be as high as 1:75 without being fatal to chinook salmon fingerlings in 122½ hours if the dissolved oxygen concentration was kept at 6.5 parts per million. Experiments were carried out by Eriksen and Townsend (1940) in the State Pollution Laboratory of the State of Washington, U.S.A., with small silver salmon of seaward migrant size. These were tested in pairs in fresh water having low dissolved oxygen concentration. The tolerance of the fish for low dissolved oxygen concentration was determined simultaneously for one fish in fresh water and another in water of the same dissolved oxygen concentration but with the addition of 1:1000 of waste sulphite liquor (Sp.Gr. 1.050). The data show that waste sulphite liquor in the concentration tested markedly affected the fish's ability to withstand low dissolved oxygen concentrations near the minimum value for that fish.

Sulphur dioxide and sulphurous acid are both harmful to fish, partly owing to their high acidity. Benson and Benson (1932) found that sulphite liquor at concentrations of less than 100 parts per million had little effect on the pH of sea water and that this effect is variable.

ANALYTICAL METHODS

The following determinations were made: temperature, salinity, sulphate, sulphite and dissolved oxygen. Temperature and salinity were determined by the standard hydrographical methods. Sulphate was determined gravimetrically as barium sulphate after oxidation with bromine water (Scott and Furman, 1939). The procedure used for sulphite was that given by American Public Health Association (1936), except that N/400 solutions were used in place of the specified N/40 solutions. Dissolved oxygen was determined by the Winkler method (American Public Health Association, 1936).

HUMBER ARM

DESCRIPTION

Humber Arm (Fig. 1) is one of the arms of Bay of Islands on the west coast of Newfoundland. Nearly 15 miles (24 km.) long and averaging $1\frac{1}{4}$ miles (2 km.) in width, it is surrounded by high, steep hills. At the head of the Arm there is a bar about three-quarters of a mile (1 km.) long where the depth of water is about 1 metre. In the remainder of the Arm the depth is around 100 metres.

The Humber River enters the Arm at the extreme east end, and during 1942 had an average flow of 10,042 cubic feet (284 cu. m.) per second, which was 3 per cent above the average for the past 26 years. Between June 25 and August 25 the tides were observed 10 times, and the greatest difference between low and high water was approximately 4.5 feet (1.4 m.). There is an outward flow on the surface, independent of tidal phase, with an estimated speed of 3 knots.

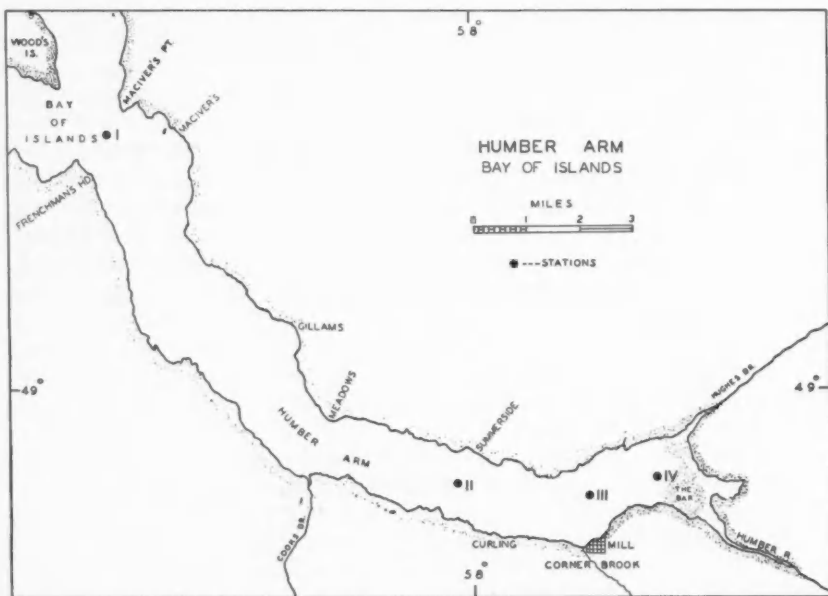


FIGURE 1. Humber Arm showing locations of stations.

The pulp and paper mills are situated at Corner Brook on the south shore of Humber Arm, about $2\frac{1}{4}$ miles (4 km.) from the head of the Arm. Opposite the mill the Arm is $1\frac{1}{4}$ miles (2 km.) wide, the depth being over 73 metres except for a short distance on either side. Thus the sewer effluents are considerably diluted soon after entering the Arm.

SAMPLING METHODS

Samples were taken at four stations as shown in Figure 1, Station I being at the mouth and Station IV at the head of the Arm. Four Nansen water-samplers, each with one Richter deep-sea reversing thermometer, were used simultaneously when taking samples which were taken at the following depths: surface, 1, 2, 4, 6, 10, 20, 40, 60 metres, and 3 metres from the bottom.

RESULTS

On August 14, 1942, samples were taken at Stations I, II and III on ebb tide. The temperature, salinity, sulphate and dissolved oxygen determinations are given in Table I and are shown in Figures 2, 3, 4 and 5, respectively. The temperature decreased rapidly from the surface down to 40 metres and slowly from 40 metres to the bottom (Fig. 2). The temperatures at these depths were: 19.20 to 20.60°C. at the surface, 1.01 to 1.50°C. at 40 metres, and -0.02 to -0.23°C. at the bottom.

The salinity increased with depth with few exceptions (Fig. 3). There was a considerable increase from the surface to 4 metres, a fair increase from 4

TABLE I. Samples from Humber Arm taken August 14, 1942, on ebb tide.

Depth	Temperature	Salinity	Sulphate	Dissolved oxygen
<i>metres</i>	<i>° C.</i>	<i>‰</i>	<i>‰</i>	<i>% sat'n</i>
STATION I				
Surface	19.50	84.89
1	...	23.75
2	...	26.55
4	16.80	29.38	2.209	89.00
6	16.37	29.88	2.222	88.36
10	15.82	30.41	2.332	89.25
20	10.17	31.04	2.330	85.26
40	1.50	31.96	2.395	75.61
60	0.74	32.10	2.457	71.80
93	-0.02	32.21	2.423	70.57
STATION II				
Surface	20.60	7.40	0.606	87.08
1	...	24.75
2	...	15.17
4	16.80	28.07	2.131	84.65
6	16.10	29.33	2.244	...
10	15.34	30.01	2.279	...
20	12.43	30.56	2.295	82.90
40	1.21	31.84	2.438	...
60	0.25	32.03	2.439	65.31
98	-0.23	32.30	2.408	53.08
STATION III				
Surface	19.20	6.40	0.498	90.61
1	...	8.16
2	...	25.30
4	...	28.02
6	15.94	29.29	2.252	85.52
10	15.03	31.36	2.262	84.27
10	10.51	30.69	2.353	83.14
40	1.01	31.81	2.401	70.41
60	-0.01	31.99	2.439	63.65
89	-0.22	32.19	2.427	55.88

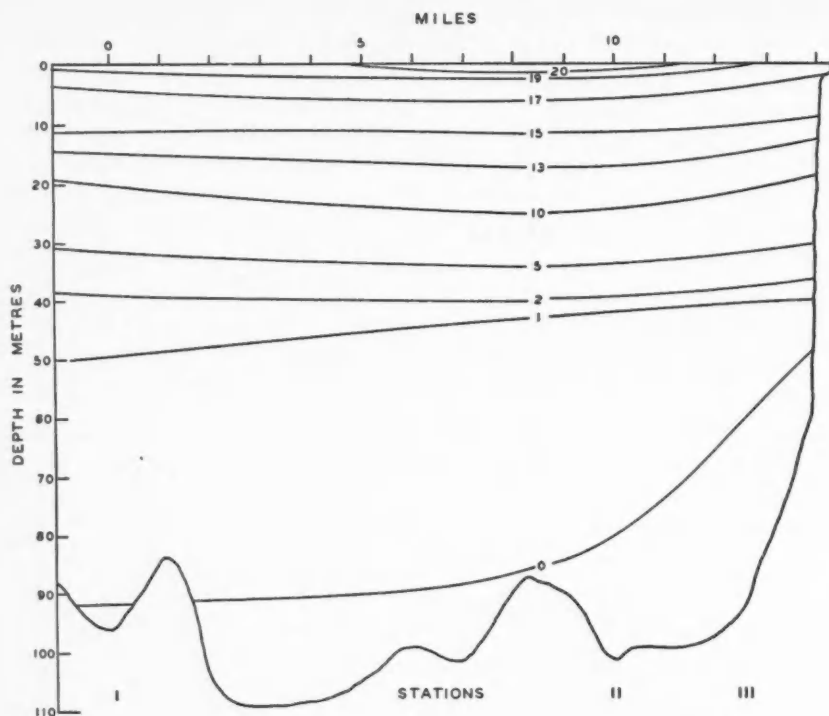


FIGURE 2. Temperature in Humber Arm on August 14, 1942, in degrees Centigrade.

metres to 40 metres, and only a slight change from 40 metres to the bottom. The salinities at these depths were: 6.40–7.40‰ at the surface, 28.02–29.38‰ at 4 metres, 31.81–31.96‰ at 40 metres, and 32.19–32.30‰ at the bottom. Results of a series of hydrographical observations on August 5–6, 1915, in the Gulf of St. Lawrence extending from Bay of Islands northwesterly to Quebec are given by Bjerkan (1919). He found that water of salinity 30–32‰ occupied most of the section from the surface down to 50 metres. At the Quebec end of the section it only reached down to 30–40 metres and near the Newfoundland coast down to 40 metres. Water of salinity less than 30‰ was only found as a thin layer at the surface at the Quebec end of the section. In our investigations in Humber Arm during August, 1942, water of salinity less than 30‰ extended from the surface down to about 10 metres at the most. Therefore the main effect of fresh water from the Humber River on the salinity of the water in Humber Arm is limited to approximately the upper 10 metres, the extent presumably varying with the season.

The amount of sulphate was determined to see if there was a large excess resulting from mill effluents. The sulphates (Fig. 4) increased rapidly from

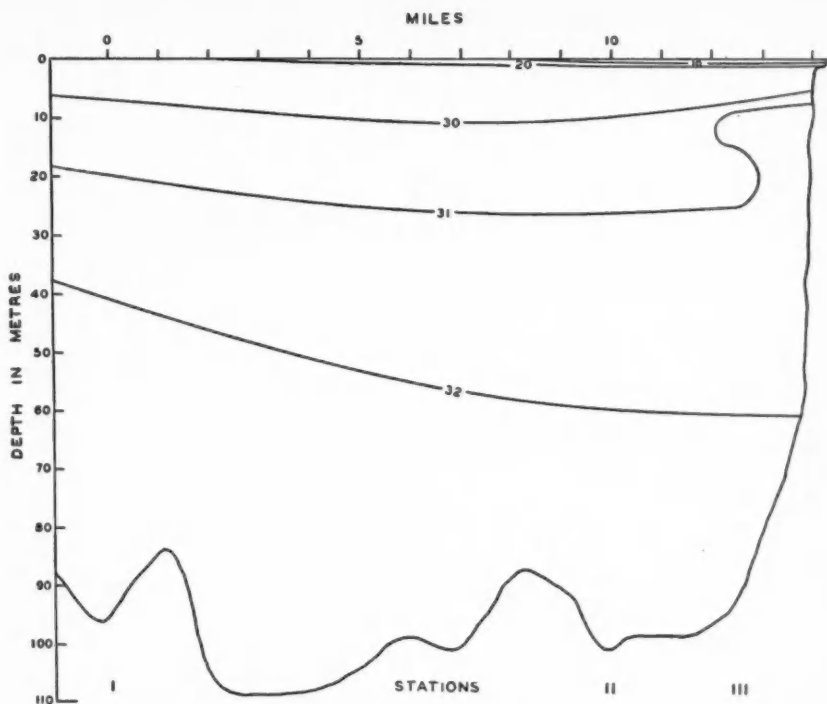


FIGURE 3. Salinities in Humber Arm on August 14, 1942, expressed as parts per thousand.

0.498–0.606‰ at the surface to 2.131–2.209‰ at 4 metres and then increased to 2.395–2.438‰ at 40 metres. Below 40 metres they changed only slightly, not more than 0.062‰. Both the salinities and the sulphates at the surface increased from the head to the mouth of the Arm (Table I and Appendix Tables VI–VIII).

Thompson, Johnston and Wirth (1931) found that the sulphate-chlorinity ratio of the oceans was 0.1395, but that this was not constant in the presence of freshwater dilution as exemplified in the Baltic Sea. By the use of the constant and the chlorinity as determined at each point, the sulphate content in parts per thousand was predicted. These values were then compared with the analytically determined values. The results are given in Table II, and show that 18.2 per cent were slightly above and the others were slightly below the predicted values. The average excess was 0.047 parts per thousand and the average deficiency –0.043 parts per thousand. In the majority of cases there was less than the predicted amount. Since there are large deposits of limestone in the Humber area it is possible that there is enough calcium in the fresh water to precipitate the seawater sulphate.

No sulphite was detected.

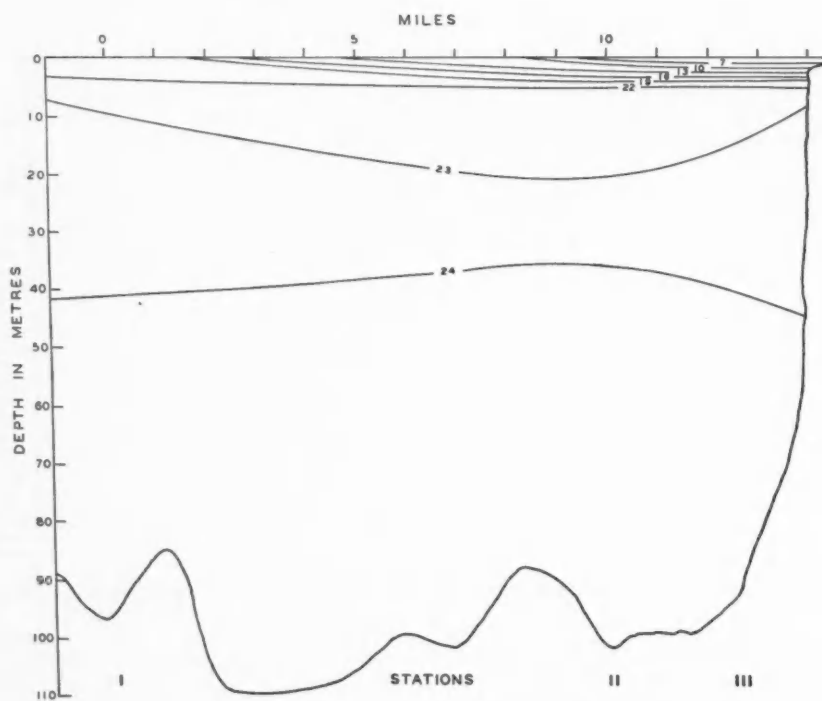


FIGURE 4. Sulphate in Humber Arm on August 14, 1942, expressed as parts per 10,000.

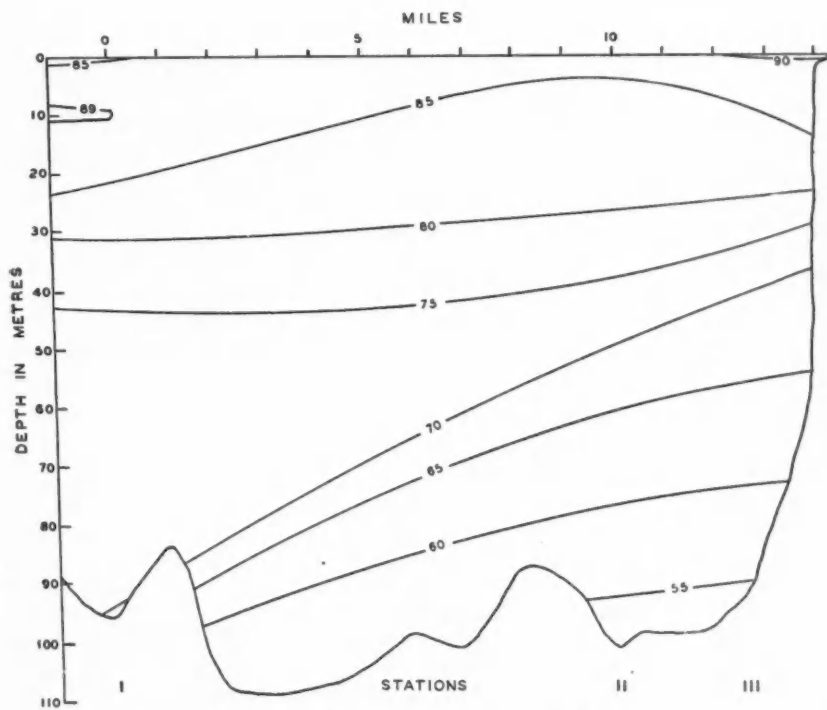


FIGURE 5. Dissolved oxygen in Humber Arm on August 14, 1942, expressed as percentage of saturation.

TABLE II. Differences between predicted and observed sulphate as parts per thousand in Humber Arm on August 14, 1942, on ebb tide.

Depth	Sulphate (parts per thousand)		
	Observed (A)	Predicted (B)	Difference (A-B)
<i>metres</i>	<i>‰</i>	<i>‰</i>	<i>‰</i>
STATION I			
Surface
4	2.209	2.255	-0.046
6	2.222	2.294	-0.072
10	2.332	2.336	-0.004
20	2.330	2.386	-0.056
40	2.395	2.459	-0.064
60	2.457	2.470	-0.013
93	2.423	2.478	-0.055
STATION II			
Surface	0.606	0.558	0.048
4	2.131	2.152	-0.021
6	2.244	2.251	-0.007
10	2.279	2.305	-0.026
20	2.295	2.348	-0.053
40	2.438	2.449	-0.011
60	2.439	2.464	-0.025
98	2.408	2.485	-0.077
STATION III			
Surface	0.498	0.480	0.018
6	2.252	2.248	0.004
10	2.262	2.411	-0.149
20	2.353	2.358	-0.005
40	2.401	2.446	-0.045
60	2.439	2.322	0.117
89	2.427	2.477	-0.050

The dissolved oxygen (Fig. 5) decreased fairly regularly with depth varying from 84.9-90.6 per cent saturation at the surface to 53.1-70.6 per cent saturation at the bottom. According to the National Resources Committee (1939) a dissolved oxygen concentration of 5 parts per million should be maintained at all times as a protection to fish life. In sea water of salinity 27‰

5 parts per million at 0°C. = 41.3 per cent saturation

5 " " " " 5°C. = 46.7 " " "

5 " " " " 10°C. = 52.3 " " "

5 " " " " 15°C. = 57.9 " " "

5 " " " " 20°C. = 66.3 " " "

These figures were calculated from data given by American Public Health Association (1936, table XV). The lowest observed value was 53.1 per cent saturation at a temperature of -0.23°C. and salinity of 32.30‰, which is greater than the amount recommended. Thus the supply of dissolved oxygen in Humber Arm was sufficient for healthy fish life. No dead or distressed fish were noticed during the investigation. It may be concluded that the 1942 operations of the mill had no deleterious effects on fish life in Humber Arm.

EXPLOITS RIVER

DESCRIPTION

The Exploits River is about 153 miles (246 km.) long and is the longest river in Newfoundland. At Grand Falls, about 10 miles (16 km.) above the head of tide, are situated the pulp and paper mills of the Anglo-Newfoundland Development Co., Ltd. The waste sulphite liquor is emptied into the river by sewer.

SAMPLING METHODS

Below the sewer outlet the river passes through a series of steep rapids and gorges before it widens into a slow, shallow river about 1½ miles (2.4 km.) from the falls. Just below the sewer the river widens and deepens into a pool. Stations I and II were taken at this pool. Station I was just at the edge of the current where the depth was 17 metres. Samples were taken at the surface, 7 metres and 14 metres. Station II was in the middle of the main current and samples were taken at 10 metres only. About 1½ miles (2.4 km.) below the sewer the river widens again, and Stations III and IV were taken here. The current divided into two at this point and one station was chosen in each. Since the depth was only 3 metres, samples were taken at 1.5 metres at both stations. Temperature, dissolved oxygen and sulphite were determined.

RESULTS

The temperatures at all stations on both September 1 and 2 are given in Table III. It can be seen that over the short stretch of river examined there was no appreciable change of temperature.

The amount of dissolved oxygen expressed as percentage of saturation is given in Table IV. Five parts per million of dissolved oxygen is needed for healthy fish life (National Resources Committee, 1939) which is equivalent to 51.2 per cent saturation on September 1 and 52.1 per cent saturation on September 2. There was only one value below these figures. That was at Station IV on September 1 when the value was 18.8 per cent saturation. On both days the amount of dissolved oxygen at Stations III and IV was less than at Stations I and II. This indicates that sulphite or other chemical or organic matter was being oxidized on its way down the river. On September 1 the dissolved oxygen concentration above the sewer (sample taken above the falls) was determined to be 82.1 per cent saturation, which was higher than any values at any of the four stations for that day. Thus the mill effluents decreased the dissolved oxygen in the Exploits River.

TABLE III. Temperatures in Exploits River in degrees Centigrade.

Station	Depth	September 1, 1942	September 2, 1942
	<i>metres</i>	<i>° C.</i>	<i>° C.</i>
I	Surface	18.3	17.0
I	7	18.3	17.0
I	14	18.3	17.0
II	10	18.3	17.0
III	1.5	18.4	17.2
IV	1.5	18.3	17.2

The amount of sulphite expressed as parts per million is given in Table V. Fish will survive in water having sulphite liquor concentration as high as 1:250, i.e. approximately 4,000 parts per million (Marsh, 1907). The amount of sulphite in this wood liquor depends on the type of wood and method of manufacture, but it would give a higher value on 1:250 dilution than those obtained on the Exploits. The highest observed amount on September 1 and 2, 1942, was 3.1 parts per million.

No dead or distressed fish were seen in or on the banks of the Exploits during the investigation. It may be concluded that the mill effluents did not seriously affect fish life in the Exploits River.

TABLE IV. Amount of dissolved oxygen in Exploits River expressed as percentage of saturation.

Station	Depth	September 1, 1942	September 2, 1942
	<i>metres</i>	<i>%</i>	<i>%</i>
I	Surface	69.53	81.23
I	7	74.52	82.06
I	14	61.18	81.45
II	10	68.05	81.82
III	1.5	57.36	80.40
IV	5.1	18.84	80.48

TABLE V. Amount of sulphite in Exploits River expressed as parts per million.

Station	Depth	September 1, 1942	September 2, 1942
	<i>metres</i>	<i>p.p.m.</i>	<i>p.p.m.</i>
I	Surface	1.1	1.7
I	7	1.6	1.7
I	14	1.7	1.2
II	10	1.5	1.8
III	1.5	3.1	0.6
IV	1.5	2.6	0.8

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APPENDIX

TABLE VI. Samples from Humber Arm taken August 4, 1942, on ebb tide.

Depth	Temperature	Salinity	Sulphate	Dissolved oxygen
<i>metres</i>	$^{\circ}$ C.	‰	‰	‰ sat'n.
STATION I				
Surface	17.90	15.48	1.251	84.06
2	...	20.04
6	...	30.27
10	...	30.72
25	4.63	30.86	2.374	83.06
STATION II				
Surface	17.80	4.09	0.373	83.38
2	15.41	29.41	2.306	86.73
6	14.97	29.92	2.360	87.69
10	14.66	30.26	2.332	88.77
25	5.92	30.97	2.460	81.89
STATION III				
Surface	18.20	3.91	...	83.62
2	15.52	29.17	2.284	84.33
6	14.84	29.86	...	87.99
10	14.83	30.23	...	87.31
25	4.97	30.95	...	77.87
STATION IV (slack water)				
Surface	17.90	4.42
2	15.50	28.60	...	84.53
6	14.70	29.79	...	85.54
10	14.50	30.85
25	4.44	30.82	...	77.14

TABLE VII. Samples from Humber Arm taken August 4, 1942, on flood tide.

Depth	Temperature	Salinity	Sulphate	Dissolved oxygen
<i>metres</i>	$^{\circ}$ C.	‰	‰	‰ sat'n.
STATION I				
Surface	18.22	16.43	1.266	82.08
2	17.27	24.07	1.923	85.78
6	15.90	30.16	2.282	89.21
10	15.77	30.56	2.316	89.74
25	11.93	30.99	2.339	85.94
STATION II				
Surface	18.92	6.97	0.498	79.36
2	15.55	29.00	2.212	86.83
6	14.97	30.12	2.262	86.90
10	14.15	30.41	2.316	87.45
25	2.76	31.44	2.365	78.61
STATION III				
Surface	18.52	5.59	0.427	84.48
2	15.45	29.35	1.977	86.08
6	14.85	30.25	2.285	87.69
10	13.69	30.41	2.339	86.10
25	2.03	31.52	2.361	74.59
STATION IV				
Surface	18.53	2.77	0.204	83.02
2	15.45	29.24	2.224	85.30
6	14.05	30.07	...	86.37
10	13.69	30.41	...	86.62
25	2.03	31.40	...	70.78

TABLE VIII. Samples from Humber Arm taken August 25, 1942, on flood tide.

Depth	Temperature	Salinity	Sulphate	Dissolved oxygen
<i>metres</i>	° C.	‰	‰	‰ sat'n.
STATION I				
Surface	16.80	27.05	2.080	81.42
1	...	28.41
2	...	29.47
4	...	29.87
6	...	30.16
10	...	30.12
20	...	30.46
40	6.73	31.20	2.360	76.47
60	0.61	32.10	2.431	71.35
93	0.15	32.25	2.351	61.97
STATION II				
Surface	16.10	3.68	0.303	80.69
1	...	15.72
2	...	24.93
4	...	27.58
6	16.70	29.47	2.211	...
10	16.58	29.94	2.234	77.84
20	16.36	30.39	2.274	85.25
40	1.65	31.77	2.378	71.32
60	0.11	31.99	2.412	61.02
98	-0.07	31.82	2.397	55.42
STATION III				
Surface	16.40	2.99	0.222	82.46
1	...	23.52
2	...	24.86
4	...	28.25
6	...	29.54
10	16.28	29.90	2.265	79.56
20	16.33	30.10	2.313	81.37
40	13.65	30.58	2.292	77.61
60	0.23	31.99	2.420	62.99
89	-0.02	32.19	2.451	61.06

TABLE IX. Differences between predicted and observed sulphate as parts per thousand in Humber Arm on August 4, 1942.

Depth	Sulphate (parts per thousand)		
	Observed (A)	Predicted (B)	Difference (A-B)
<i>metres</i>	$\frac{\text{‰}}{\text{‰}}$	$\frac{\text{‰}}{\text{‰}}$	$\frac{\text{‰}}{\text{‰}}$
(a) Ebb tide			
		STATION I	
Surface	1.251	1.177	0.074
25	2.374	2.376	-0.002
		STATION II	
Surface	0.373	0.314	0.059
2	2.306	2.261	0.045
6	2.360	2.302	0.058
10	2.332	2.328	0.004
25	2.460	2.384	0.076
		STATION III	
2	2.284	2.242	0.042
(b) Flood tide			
		STATION I	
Surface	1.266	1.248	0.018
2	1.923	1.840	0.083
6	2.282	2.316	-0.034
10	2.316	2.349	-0.033
25	2.339	2.382	-0.043
		STATION II	
Surface	0.498	0.524	-0.026
2	2.212	2.225	-0.013
6	2.262	2.314	-0.052
10	2.316	2.336	-0.020
25	2.365	2.418	-0.053
		STATION III	
Surface	0.427	0.429	-0.002
2	1.977	2.254	-0.277
6	2.285	2.324	-0.039
10	2.339	2.336	0.003
25	2.361	2.424	-0.063
		STATION IV	
Surface	0.204	0.212	-0.008
2	2.224	2.244	-0.020

TABLE X. Differences between predicted and observed sulphate as parts per thousand in Humber Arm on August 25, 1942, on flood tide.

Depth	Sulphate (parts per thousand)		
	Observed (A)	Predicted (B)	Difference (A-B)
<i>metres</i>	<i>‰</i>	<i>‰</i>	<i>‰</i>
		STATION I	
Surface	2.080	2.073	0.007
40	2.360	2.398	-0.038
60	2.431	2.470	-0.039
93	2.351	2.481	-0.130
		STATION II	
Surface	0.303	0.281	0.022
6	2.211	2.262	-0.051
10	2.234	2.300	-0.066
20	2.274	2.335	-0.061
40	2.378	2.443	-0.065
60	2.412	2.461	-0.049
98	2.397	2.447	-0.050
		STATION III	
Surface	0.222	0.228	-0.006
10	2.265	2.297	-0.032
20	2.313	2.312	0.001
40	2.292	2.350	-0.058
60	2.420	2.461	-0.041
89	2.451	2.477	-0.026
		STATION IV (ebb)	
Surface	0.531	0.990	-0.459
10	1.482	2.304	-0.822
40	2.349	2.389	-0.040
54	2.386	2.383	0.003

Atlantic Cod Populations along the Southern Canadian Mainland as shown by Vertebral Count Studies¹

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ABSTRACT

Analysis of vertebral counts of 28,097 cod (*Gadus callarias* L.) in 184 samples from the Canadian mainland coast demonstrates some segregation of inshore and offshore populations and little mixing between the cod on various sections of the coast. Four populations are recognized in the Gulf of St. Lawrence. Three offshore populations and at least four inshore populations are also recognized along the south coast of Nova Scotia. Seasonal migrations northward in summer and southward in winter are indicated by changes in vertebral numbers. Small cod (less than 2½ lb.) exhibit less variability in vertebral number than larger ones, suggesting increased mixing with growth.

INTRODUCTION

THE FISHERY for cod (*Gadus callarias* L.) of the northwest Atlantic ocean dominates the fisheries for other species. Fishermen from ten nations land some two billion pounds annually. The principal grounds are found off Greenland, Newfoundland and the Canadian mainland. Cod populations of the last area are described in the present paper.

The Fisheries Research Board of Canada carried out an intensive program of tagging and vertebral-count studies during the period 1933 to 1941 in order to define the cod stocks off the Canadian mainland. Such knowledge of the division of cod stocks is of primary importance in the development of a sound management policy. The populations are here defined on the basis of vertebral-count studies.

METHODS

SOURCE OF MATERIALS

This account deals with the analysis of 184 samples of cod (28,097 fish) which were graded before landing into three market size categories: "scrod" (under 2½ lb.), "market" (2½ to 10 lb.) and "steak" (over 10 lb.).

Each vertebral count is the total number of vertebrae, excluding the last flattened vertebra (urostyle). Small numbers of cod with fused vertebrae were discarded. Skeletons discarded from filleting tables and split fish, ready for saiting, were used in most cases.

The samples were taken at different seasons during the period 1935 to 1940. The sampling stations were scattered along the coasts of New Brunswick, Nova Scotia, Prince Edward Island and Gaspé. For convenience of analysis, four

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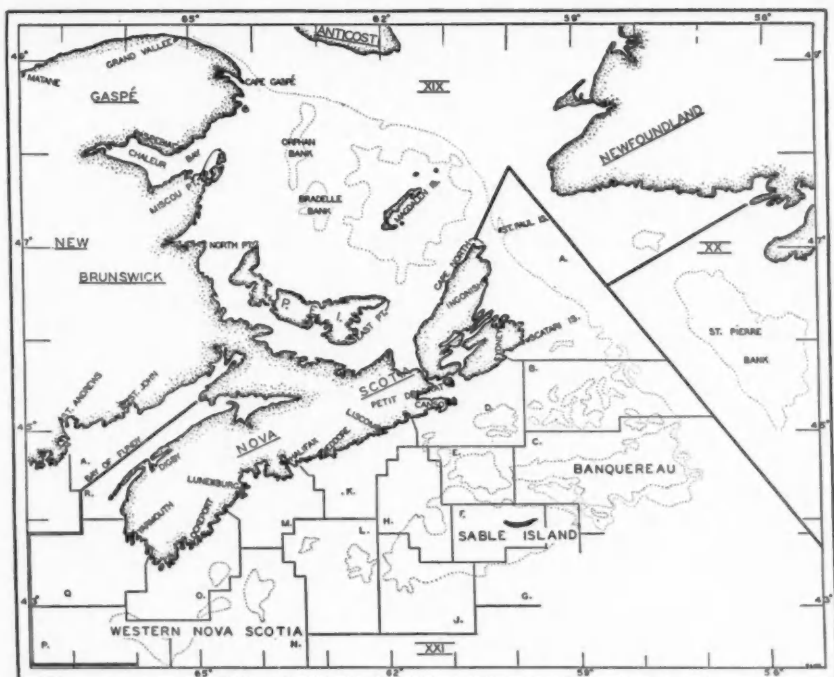


FIGURE 1. The Canadian Atlantic area showing the regions where the vertebral collections were made.

seasons have been used—February to April (spawning period along the Nova Scotia coast), May to July, August to October and November to January. Similarly, samples were assigned to twelve geographic categories based on a division of grounds which was agreed upon by the North American Council on Fishery Investigations (Fig. 1 and Table I).

TREATMENT OF THE DATA

The 184 samples mentioned previously have been classified by year of sample (6 categories), geographical origin of sample (12 categories) and commercial grading by size of fish (3 categories). The mean vertebral count of each such sample obtained and the number in each sample are shown in the Appendix. This places the basic data on record for comparisons other than are to be made in this paper. The average variance of these distributions is about 0.77 and thus the standard error of any particular mean would be about $\sqrt{0.77/n}$ where n is the number in the sample; for example, about 0.1 for a sample of 75.

The main aim of this paper is to evaluate differences that could be attributed to geographical location, season of capture and size of fish. A preliminary

TABLE I. Comparisons of vertebral counts among both seasons and geographical areas (Seasons: 1—Feb., Mar., Apr.; 2—May, June, July; 3—Aug., Sept., Oct.; 4—Nov., Dec., Jan.). The means have been adjusted for year-to-year variation, as described in the text.

Season								
1			2		3		4	
Count		<i>n</i>	Count		Count		Count	
			<i>n</i>		<i>n</i>		<i>n</i>	
MARKET COD								
Gaspé	53.56	261	52.74	104	53.14	24
Bay Chaleur	52.89	628	52.86	243
P.E.I., N.B.	52.75	183	52.65	312	52.45	200
Cape Breton W.	52.70	179	52.97	183	52.94	290
XXI A	52.92	100	52.92	595	53.11	478	52.94	718
XXI D	53.02	236	53.20	373	53.28	208
XXI BC	53.15	896	53.28	502	53.18	510	53.11	1074
XXI EFGHJL	53.00	2101	53.00	1407	52.77	897	52.96	1378
XXI KM	52.93	745	52.87	568	52.86	515	52.91	897
XXI OPN	52.72	753	52.88	1093	52.67	510	52.81	1694
XXI QR	52.49	80	52.58	478	52.68	187	52.50	733
St. Pierre Bk.	52.83	399	52.77	181	52.72	252
Mean for "markets"—52.91								
STEAK COD								
Gaspé	53.28	75	53.08	24	53.42	24
Bay Chaleur	52.68	482	52.61	166
P.E.I., N.B.	52.19	395	52.39	185
Cape Breton W.	52.58	43	53.00	18
XXI A	52.90	186
XXI D	53.20	76	52.91	22
XXI BC	53.35	150	53.23	249	53.24	100
XXI EFGHJL	53.34	1024	53.08	44	53.28	79	53.23	101
XXI KM	52.96	74	53.10	15
XXI OPN	53.39	50
XXI QR	52.79	170
St. Pierre Bk.	52.53	108
Mean for "steaks"—52.96								

examination of the data in the Appendix indicated that such comparisons were complicated by year-of-capture differences. A first approximation correction for year-of-capture differences was made by applying an arithmetic correction to each of the years to equalize year means over places and seasons occurring in all years, and applying this same correction to all the data. Quite arbitrarily the mean for "markets" for season 1 in area XXI EFGHJL was corrected to 53.00 and all other categories were adjusted to conform with this. The data available on small fish (scrod) were not extensive enough to make useful comparisons. The result of this rough correction for year of capture differences is shown in Table I. The slight difference in grand mean vertebral counts between "steaks" and "markets" is due, at least in part, to the year-of-capture correction being made on each group independently and to the fact that the same categories of year, location and season are not in common throughout the whole of both series.

These corrected means are comparable directly in any desired pair. The significance of a difference depends upon the spread about the means and sample sizes. Table II (significant differences) is the difference to be expected by chance once in twenty such comparisons. It should be remembered, therefore, that about

5% of the random comparisons, even though exceeding the amount in Table II, may not reflect real population differences.

One aspect of the available data on scrod size is shown in Table III. The samples for market and steak cod for the same places, seasons and years for which scrod samples were available are shown. The columns marked "mean variance" are the means of the variances of all the samples making up the cell and not the variances of the mean shown in the preceding columns. Even though these data are neither complete nor extensive enough to bear critical examination for statistical significance, the lower mean variance of the scrod samples is reasonable.

TABLE II. Significant differences in mean vertebral number (at 5% level), for sample sizes (n_1 and n_2) of 25 to 1000, when average variance is 0.77.

n_2	n_1					
	25	50	100	200	500	1000
25	0.49	0.42	0.39	0.37	0.35	0.35
50	...	0.35	0.30	0.27	0.26	0.25
100	0.24	0.21	0.19	0.18
200	0.17	0.14	0.13
500	0.11	0.09
1000	0.08

TABLE III. Mean vertebral counts and variances of all cod sampled.

Year	Steak			Market			Scrod		
	Mean	Mean variance	n	Mean	Mean variance	n	Mean	Mean variance	n
1935	52.81	0.616	243	52.98	0.725	3263	52.72	0.789	76
1936	53.28	0.667	340	52.95	0.742	4410	52.81	0.435	208
1937	53.07	0.825	996	53.00	0.734	4735
1938	52.78	0.779	680	52.78	0.950	3405	52.52	0.625	145
1939	52.82	0.943	991	52.77	1.215	4480	52.64	0.884	118
1940	52.81	0.905	674	52.92	0.794	3397	52.20	0.750	25
Mean	52.93	0.79		52.90	0.86		52.58	0.69	

RESULTS

A cline of vertebral counts was observed in inshore waters along the Nova Scotia coast; low counts were found off Digby in the west and high counts off Canso in the east. In most cases, the cod of any one of the inshore areas are distinct from those of adjacent areas.

Data from Nova Scotian offshore banks show a similar cline of vertebral counts, increasing from west to east. Three distinct offshore populations are recognized, namely, western Nova Scotia, Sable Island and Banquereau.

In the southwestern Gulf of St. Lawrence, vertebral counts increase from south to north. In general, there appear to be four populations of cod south of

the Laurentian Channel; a Cape Breton population, a Prince Edward Island population, a Chaleur Bay population and a Gaspé population.

Small seasonal changes in vertebral counts reflect seasonal movements of cod. Vertebral counts increase during summer months off Cape Breton and during winter months on Nova Scotian banks. A northerly movement of fish during warm months and a southerly movement during cold months are indicated.

St. Pierre Bank, immediately east of the deep-water Laurentian Channel, has a cod population which is sharply distinct from those of the nearest Nova Scotian grounds. The low vertebral counts of St. Pierre Bank cod are comparable with those of western Nova Scotian and Prince Edward Island populations.

The lower mean variances of "scrod" cod suggest that local and relatively distinct groups of young cod become less distinct through mixing as they grow older and larger.

DISCUSSION

This analysis of vertebral counts has extended our knowledge of cod populations of the Canadian mainland area. Earlier accounts (McKenzie, 1939, 1940) described three distinct cod populations off Nova Scotia, including the autumn-spawning population in the Halifax area with its very low vertebral counts. These results indicate that fairly independent populations of cod exist in other areas around the Canadian mainland coast and that mixing of fish from different locations is not general.

The deductions based on vertebral numbers support and extend those of tagging studies carried out concurrently (McKenzie, MS). Most tag returns are from close to the tagging area, but occasional recoveries show extensive migrations. The vertebral studies demonstrate that the longer migrations are either so ordered or involve such a small proportion of the fish that differences between populations in adjacent regions are not destroyed. The northward summer movement and southward winter movement of cod suggested by the vertebral counts are confirmed by tagging.

ACKNOWLEDGMENTS

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APPENDIX

SAMPLE MEANS AND SAMPLE SIZES, COD VERTEBRAL COUNTS
(Three-month seasons are designated as 1, 2, 3 and 4, starting
with February-April)

YEAR 1935												
Area	Steak				Market				Scrod			
	1	2	3	4	1	2	3	4	1	2	3	4
XXI A	53.19 69	53.19 100	52.89 97				
XXI D	53.24 91	...				
XXI BC	53.20 199	52.98 100	53.13 300				
XXI EFGHJL	52.95 22	...	52.89 79	53.05 467	52.89 501	53.00 301				
XXI KM	53.03 169	52.87 100	52.94 203	52.35 26	...
XXI OPN	53.00 50	52.69 49	52.91 202	...	53.03 38	52.92 50
XXI QR	...	52.62 92	52.52 101				
St. Pierre Bank	52.72 100	53.11 76	...				
YEAR 1936												
Area	Steak				Market				Scrod			
	1	2	3	4	1	2	3	4	1	2	3	4
P.E.I., N.B.	52.31 100				
Cape Breton W.	52.80 97				
XXI A	53.18 99	53.00 222				
XXI D	53.39 118				
XXI BC	53.21 446	53.12 101	53.50 110	...				
XXI EFGHJL	53.31 296	53.05 44	53.04 510	52.97 100	52.82 101	52.94 709				
XXI KM	52.94 100	53.03 100	...	52.96 304				
XXI OPN	52.78 98	52.96 298	52.44 101	52.84 300	52.91 138
XXI QR	52.48 196	...	52.46 660	52.61 70	...
St. Pierre Bank	52.82 100				

APPENDIX (Continued)

YEAR 1937												
Area	Steak				Market				Scrod			
	1	2	3	4	1	2	3	4	1	2	3	4
Gaspé	53.08 24	53.18 38	53.29 76				
Bay of Chaleur	52.90 10	53.21 133	...				
P.E.I., N.B.	...	52.15 74	52.00 16	52.40 58	...				
Cape Breton W.	...	52.86 14	53.00 18	52.62 85	52.93 83	...				
XXI A	...	52.38 21	53.07 100	53.02 131	53.13 179	...				
XXI D	52.91 22	53.07 100	53.24 78	...				
XXI BC	53.55 100	...	53.26 99	53.24 100	53.14 300	...	53.14 102	53.24 199				
XXI EFGHJL	53.34 301	53.15 808	52.87 202	52.89 295	53.06 101				
XXI KM	52.96 74	...	53.20 15	...	53.15 473	52.22 100	52.77 196	53.01 97				
XXI OPN	52.90 306	...	52.81 310	...				
XXI QR				
St. Pierre Bank	52.63 108	52.71 105	...				

YEAR 1938												
Area	Steak				Market				Scrod			
	1	2	3	4	1	2	3	4	1	2	3	4
Gaspé	53.00 24	53.42 100	53.44 66	...				
Bay of Chaleur	...	52.64 143	52.51 156	52.75 277	52.45 110	52.73 33	...
P.E.I., N.B.	...	52.26 100	52.59 97	...				
Cape Breton W.	52.87 193				
XXI A				
XXI D	53.03 90				
XXI BC	53.37 100	53.40 101	...	52.92 89				
XXI EFGHJL	53.26 156	53.15 101	52.84 100	52.81 199	...	52.98 267				
XXI KM	52.44 71	...	52.86 119	52.73 193				
XXI OPN	52.82 99	52.56 589	52.50 100	...
XXI QR	52.52 187	52.45 199	52.25 12	
St. Pierre Bank	52.80 99	...	52.25 60				

APPENDIX (Continued)

YEAR 1939												
Area	Steak				Market				Scrod			
	1	2	3	4	1	2	3	4	1	2	3	4
Gaspé	...	53.31 75	53.46 161				
Bay of Chaleur	...	52.60 339	52.69 285				
P.E.I., N.B.	...	52.11 92	52.48 69	52.66 157	52.46 100				
Cape Breton W.	...	52.38 29	52.82 94				
XXI A	...	53.11 115	53.29 95	53.22 100	52.83 198	...	52.64 95
XXI D	...	53.13 76	53.01 136				
XXI BC	53.22 100	53.26 100	53.20 98	53.11 487				
XXI EFGHJL	53.27 96	52.92 270	53.05 200				
XXI KM	52.80 101	53.02 99	53.08 100	52.94 100	52.61 23	...
XXI OPN	52.61 300	52.70 398	...	52.54 374				
XXI QR	52.48 100	...	52.36 233				
St. Pierre Bank	52.71 194				

YEAR 1940												
Area	Steak				Market				Scrod			
	1	2	3	4	1	2	3	4	1	2	3	4
Bay of Chaleur	52.96 200				
P.E.I., N.B.	...	52.31 129	52.55 100	52.67 183	52.20 25
Cape Breton W.	53.05 100	...				
XXI A	...	52.68 50	52.66 300	...	52.90 201				
XXI D	53.17 204	...				
XXI BC	...	53.36 50	...	53.26 50	53.14 188	53.20 100	53.15 100	53.29 99				
XXI EFGHJL	53.54 153	52.92 413	53.13 239				
XXI KM	53.08 100				
XXI OPN	52.98 195	...	53.02 393				
XXI QR	...	52.74 78	52.65 182	...	52.47 100				
St. Pierre Bank	52.82 100				

Measuring Seepage through Salmon Spawning Gravel¹

BY R. A. POLLARD²

Pacific Oceanographic Group

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ABSTRACT

The rate of oxygen supply to salmon eggs incubating in a stream bed depends on the oxygen concentration in the groundwater and the rate of seepage through the redd. Wickett (1954) devised a simple field method of both sampling the groundwater for the determination of its dissolved oxygen content and measuring the seepage rate, using one tool, a standpipe. The theory of seepage is outlined to show the factors governing the velocity of flow through a redd. Alternative ways of measuring this velocity were examined; the best one is a modification of Wickett's procedure using a similar standpipe. A new field procedure for measuring the oxygen concentration and groundwater seepage rate in a stream bed is recommended.

INTRODUCTION

IN ALL STREAMS part of the water flows above the bed and part flows through the ground under the bed and in the banks. Salmon spawn in any apparently suitable gravel where the stream is adequately deep. But it is the invisible groundwater flow which determines whether the stream is suitable for a redd. Wickett (1954) has shown that salmon eggs incubating in a stream gravel require oxygen, which must be supplied by a continuous flow of aerated water; otherwise they will die.

The groundwater and the surface water are distinct. The groundwater loses its oxygen to humus, whereas the surface is continually aerated; the surface stream flows much faster than the groundwater, which just seeps through the gravel.

The supply of oxygen to a redd depends on its concentration in the groundwater and on the rate at which this water flows through the gravel. If the oxygen concentration O of the groundwater and its velocity V through the gravel are known, then the rate of oxygen supply to a redd OV can be computed, and this

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product should be useful in predicting whether eggs in that redd will live or die.

The biologist assessing the suitability of a stream for spawning salmon must travel on foot, carrying all his equipment on his back; he has to scramble over rocks and under bushes. His equipment should be light and compact yet rugged. Since the oxygen supply may vary from one redd to another adjacent redd, not just one value is sought, but several to give an average over the whole spawning

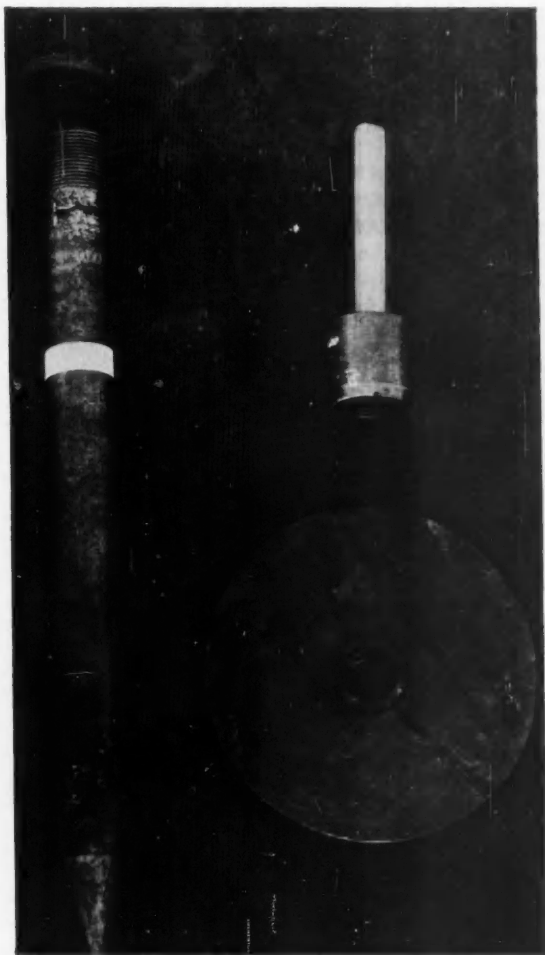
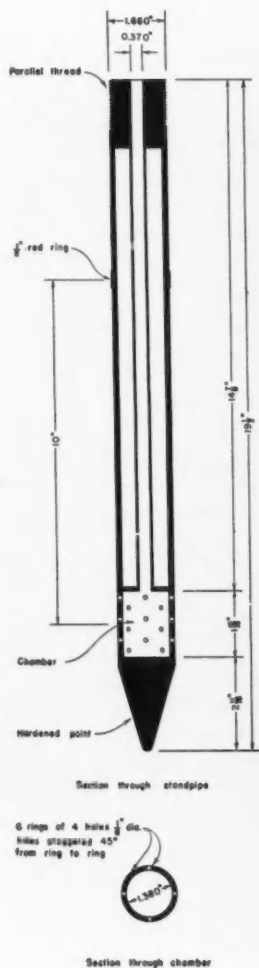


FIGURE 1. Cross-sectional drawing of standpipe, and photograph showing standpipe with driving cap, brass disc, and extension tube.

area of the stream bed under investigation. So the method must be simple and quick—even at the expense of precision. In the field, the biologist wants to measure, with only moderate accuracy, the oxygen supply to a large number of redds in a short time. Lastly, the equipment itself must be simple and reproducible so that broken parts may be repaired or replaced in isolated communities; it should be the product of a machine shop, not of a jeweller.

Wickett (1954) has devised a practical method of measuring both O and V to meet these requirements. His original equipment and procedure have been modified as a result of the laboratory investigation herein reported. A hollow pipe, pointed, and with a number of fine holes around the bottom is driven ten inches into the stream bed, the average depth the salmon lay their eggs. This *standpipe* (Fig. 1) is tantamount to a well sunk into the bed through the surface water and gravel. A sample of groundwater can be withdrawn uncontaminated by surface water for the determination of its oxygen content. Then the groundwater flow in the stream bed can be measured indirectly in two steps; first the permeability of the gravel is found by measuring the rate of inflow of groundwater when water is pumped out of the standpipe, and second, the hydraulic gradient is measured by observing the rate at which dye inside the standpipe fades by dilution with clear groundwater. From these two quantities, permeability and gradient, the velocity is calculated. By this method the oxygen supply to a redd can be measured in an hour with equipment weighing only 30 pounds.

LIST OF SYMBOLS

- A Cross-section area of flow (e.g., in a permeameter).
- C Concentration of dye at any instant in the chamber of the standpipe (colour units).
- C₀ Initial concentration of dye in the chamber of the standpipe (colour units).
- K Darcy's coefficient of permeability.
- N_R Reynolds' number.
- O Concentration of dissolved oxygen in the groundwater (mg./liter).
- P A position in a stream bed.
- Q Volume rate of discharge of a stream or permeameter.
- S Hydraulic gradient.
- T Temperature.
- U A number representing the size distribution of particles in the stream gravel.
- V Apparent velocity of the groundwater.
- Z A number representing the shape of particles in the stream gravel.
- a Fraction of flow that is laminar.
- b Fraction of flow that is turbulent.
- c (Table II).
- d Diameter of particles in a stream bed.
- e A number representing surface roughening of particles in a stream bed.
- f() Function of ().
- f (Table II).

- g Gravity.
- h, h_1, h_2 Heights above a reference level in a stream bed.
- h A small interval of height.
- h Pressure head drop in a specified length (l).
- l Length.
- m (Table II).
- n Natural number (Table II).
- p Porosity of a stream bed.
- p Pressure head drop in a length (l).
- p A small pressure head, suction head.
- q Rate of pumping (cc./minute).
- t Time interval from some arbitrary instant.
- v Absolute velocity of water through orifices in the gravel.
- α Fraction of the volume of water in the standpipe chamber exchanged per unit time.
- θ An exponent (of porosity).
- μ Absolute viscosity.
- ρ Density.
- ψ Resistance coefficient.

THEORY OF FLOW THROUGH GRAVEL

DEFINITIONS

The flow of any liquid may be either *laminar* or *turbulent*. In laminar flow the individual molecules of the liquid are considered never to cross each other's path. In turbulent flow volumes of the liquid cross and re-cross each other's path, though within each volume the flow may be laminar. For example, the rise of sap in a tree is laminar whereas an ocean current is turbulent.

A porous medium which transmits a fluid, either liquid or gaseous, is said to be *permeable*. Thus, felt and sand are permeable, whereas glass and clay are impermeable.

The *porosity* of a granular material is the ratio of the volume of the voids to the total volume of solids plus voids. The gradation of the grains of a granular material determines the number and linear dimensions of the voids through which the liquid flows and largely determines its porosity.

Even if a permeable material is saturated there can be no flow without a pressure difference across the material in the fluid. The permeability permits the flow but the pressure difference causes the flow. If water is to flow through gravel, then the groundwater pressure upstream must exceed the pressure downstream at the same elevation. The pressure head drop, or head loss, per unit length in the direction of flow is the slope of the hydraulic grade line, or *hydraulic gradient*.

The *apparent velocity* sometimes called the superficial or macroscopic velocity, is the rate of seepage expressed as the volume of liquid flowing per unit time through a unit area (of solids plus voids) normal to the direction of flow. The *true*, or *pore velocity* is the actual velocity of flow through the interstitial spaces, and differs from pore to pore.

DARCY'S LAW

The apparent velocity V of flow through a prism of granular material depends upon the pressure head drop Δh in the length L of the prism, the density ρ and the absolute viscosity μ of the fluid, the diameter d of the particles, the porosity p of the material, the acceleration of gravity g , the height e of the surface roughening of the particles, their shape Z , and upon their size distribution U . By the suitable choice of a system of definition variables Z and U may be made dimensionless. Thus

$$0 = f(\Delta h, V, \rho, \mu, L, d, p, g, e, Z, U). \quad (1)$$

According to Buckingham's π theorem, if we assume only that the 11 variables are related by a dimensionally homogeneous equation, f is not actually a function of the 11 separate variables but rather a function of a complete set of dimensionless products of the variables (Langhaar, 1951). One such set consists of $\frac{\Delta h}{d}$, the Reynolds' Number $\frac{Vd\rho}{\mu}$, the Froude Number $\frac{V^2}{gd}$, and $\frac{L}{d}$, $\frac{e}{d}$, p , Z , and U . Therefore

$$0 = f\left(\frac{\Delta h}{d}, \frac{Vd\rho}{\mu}, \frac{V^2}{gd}, \frac{L}{d}, \frac{e}{d}, p, Z, U\right). \quad (2)$$

Rose (1945) experimentally determined the value of this function for the flow of any incompressible fluid through a bed of perfectly smooth equal-sized spheres, using lead balls and so eliminating the variables $\frac{e}{d}$, Z , and U , with the following approximate³ result

$$\frac{\Delta h}{d} = \psi \cdot \frac{V^2}{gd} \cdot \frac{L}{d} \cdot \left(\frac{p}{0.40}\right)^{-4} \quad (3)$$

where ψ is a function of the Reynolds' Number, called the resistance coefficient. It is presumed that Rose's result for flow through a bed of smooth equal-sized spheres may be extended to any granular material by multiplying Equation 3 by unknown functions of $\frac{e}{d}$, of Z , and of U ⁴. Thus:

$$\frac{\Delta h}{d} = \psi \cdot \frac{V^2}{gd} \cdot \frac{L}{d} \cdot \left(\frac{p}{0.40}\right)^{-4} \cdot f\left(\frac{e}{d}\right) \cdot f(Z) \cdot f(U). \quad (4)$$

From Rose's curve relating the resistance coefficient and Reynolds' Number, for any Reynolds' Number below 10, the resistance coefficient is inversely

³Rose points out that the porosity factor in Equation 3 is not really so simple; the exponent varies with porosity itself (Fig. 18).

⁴Experiment shows that the porosity factor depends upon the shape also, which invalidates this presumption. See the section entitled "Variation of permeability with porosity".

proportional to the Reynolds' Number, which is indicative of laminar flow, and the value of ψ is:

$$\frac{1200}{\frac{Vd\rho}{\mu}}$$

Substituting this into Equation 4 and solving for the velocity V , we get

$$V = \frac{gd^2}{1200 \frac{\mu}{\rho}} \cdot \left(\frac{p}{0.40} \right)^4 \cdot \frac{1}{f\left(\frac{e}{d}\right)} \cdot \frac{1}{f(Z)} \cdot \frac{1}{f(U)} \cdot \frac{\Delta h}{L} \quad (5)$$

For laminar flow of any given incompressible liquid through a bed of any given granular material the apparent velocity V is proportional to the hydraulic gradient $\frac{\Delta h}{L}$, or S , because the first five terms on the right of Equation 5 are constants, that is,

$$V = KS. \quad (6)$$

Equation 6 is known as *Darcy's Law*. The constant of proportionality K is called *Darcy's coefficient of permeability* or more simply the *permeability*. The permeability K is defined as the apparent velocity V per unit hydraulic gradient S and has the dimension $\left[\frac{L}{T} \right]$. K varies with the physical properties of both the granular material and the liquid—precisely as shown by Equation 5.

Again, from Rose's curve, the resistance coefficient at any Reynolds' Number above 10,000 is constant, indicative of fully developed turbulent flow, and the value of ψ is roughly 13. Substituting this into Equation 4, for fully developed turbulent flow of any incompressible fluid through a bed of any given granular material, we get the velocity squared proportional to the gradient, that is,

$$V^2 = K'S. \quad (7)$$

When the flow through some of the interstitial passages is laminar and turbulent through others, the velocity is related to the gradient by the equation

$$S = \frac{a}{K} V + \frac{b}{K'} V^2 \quad (8)$$

where a is the fraction of the total flow that is laminar and b is the fraction that is turbulent, both unknown.

Darcy (1856) discovered the linear relation between V and S in experiments on water seeping through sand filters. Other pioneers in hydrology, notably Dupuit (1863), verified this relation for soils. Poiseuille (1846) calculated the laminar flow through a uniform circular tube from the viscosity and density of the liquid and size of the tube and showed that Darcy's Law applied. It is reasonable, therefore, to expect that Darcy's Law holds in most water seepage problems, for the passages are but a myriad of interlaced capillary tubes, provided the Reynolds' Number is low enough to ensure laminar flow. However, until demon-

strated by experiment, we could not assume that Darcy's Law applies to ground-water seepage through a salmon redd because, stream gravel grains being larger than soil particles, the Reynolds' Number is likely to be higher in a redd than in earth or sand.

By running water through troughfulls of various stream gravels, measuring the apparent velocities of seepage and observing the corresponding gradients, we have shown that the flow through any salmon spawning gravel is usually wholly laminar, infrequently mixed laminar and turbulent, but never wholly turbulent. Thus Darcy's Law usually applies to groundwater flow through a redd, so the apparent velocity V may validly be computed from the permeability K and the gradient S measured separately. It happens that both K and S can be measured by means of the standpipe, in addition to the oxygen concentration O .

EFFECT OF ROUGHNESS, SHAPE AND GRADATION ON PERMEABILITY

The permeability of a bed of granular material could presumably be calculated from the physical properties of the bed and the liquid if $f\left(\frac{e}{d}\right)$, $f(Z)$, and $f(U)$ were known.

Nikuradse (1933) has shown that the laminar flow through pipes is independent of the wall roughness, and hence $f\left(\frac{e}{d}\right)$ may legitimately be considered unity in Equation 4.

Particle shape affects the permeability of a bed of granular material mainly in that it affects its porosity; the more angular the particles the greater the "bridging" between the solids and hence the greater the porosity of the bed. If all other variables are held constant, including the porosity, particle shape still affects the permeability; the more angular the particles, the more irregularly shaped and tortuous the interstitial passages, and hence the greater the hydraulic resistance of the bed. $f(Z)$ is this independent effect of particle shape. Heywood (1937) has defined a significant way of expressing the shape Z . Carman (1938) found by experiment, holding constant all other variables in Equation 1, that Δh is porportional to Z^2 , and, since by Heywood's definition the shape of a sphere is 6, $f(Z)$ equals $\left(\frac{Z}{6}\right)^2$.

It follows now from Equations 5 and 6 that the permeability may be expressed

$$K = \frac{gd^2}{1200 \frac{\mu}{\rho}} \cdot \left(\frac{p}{0.40}\right)^4 \cdot \frac{1}{\left(\frac{Z}{6}\right)^2} \cdot \frac{1}{f(U)} \quad (9)$$

From Equation 9 we can calculate the permeability of a bed of equigranular particles of any size, shape and roughness to the flow of a liquid of any viscosity and density; the only restriction is that the particles be of equal size, wherefore $f(U)$ is unity.

TABLE I. Properties of gravel beds tested in the laboratory. (Gravels composed of the same particles and differing only in porosity are grouped together.)

Gravel	Description	Porosity		Average permeability at 10° C. cm./hour
		By filling	By draining	
Pea	A pea-sized, unigranular gravel placed loosely in trough.	...	0.325	32,000
1	A random gravel from Nile Creek placed loosely in trough.	...	0.139	10,500
2	Gravel 1 with 50% sand and silt added. Gravel placed loosely in trough.	...	0.147	670
3	A mixture of sand and gravels from various creeks, the composite equivalent to an equal mixture of gravels 1 and 2. Gravel placed loosely in trough.	...	0.154	4,800
4	Gravel 3 compacted in trough by tamping.	0.104	0.066	1,600
5	Gravel 4 with stones larger than 2 in. screened out. Gravel placed loosely in trough.	0.196	0.157	2,000
6	Gravel 5 compacted in trough by tamping.	0.122	0.109	810
7	Gravel 6 with about 10% fines added. Gravel placed loosely in trough.	0.127	0.122	730
8	Gravel 7 compacted in trough by tamping.	0.088	0.089	180
9	Gravel 8 compacted in trough by tamping.	...	0.066	77
10	Gravel 9 compacted in trough by tamping.	0.053	...	50
11	Gravel 10 removed from trough and replaced loosely.	370
12	Gravel 11 with about 10% pea gravel and 10% coarser random gravel added. Gravel placed loosely in trough.	...	0.123	1,300
13	Gravel 12 compacted in trough by tamping.	0.072	0.080	230
14	Gravel 13 with about 15% pea gravel added. Gravel placed loosely in trough.	0.164	0.151	2,100

To test this, the permeability of a uniform pea-sized gravel (Table I), 94 per cent of which lay within a size range of four times, was both calculated and measured in a permeameter. Its grading curve (Fig. 2) shows that the gravel is closely enough graded to be considered unigranular with a mean particle size about 0.02 ft. The porosity⁵ measured 0.325+, and was taken at 0.35. Shape Z, by Heywood's definition, measured 9.4. For water at 10°C., the kinematic viscosity $\left(\frac{\mu}{\rho}\right) = 1.411 \times 10^{-5}$ ft.²/sec. When these values are substituted into

Equation 9, K is calculated to be 0.18 ft./sec. or 20,000 cm./hr. This is a fair prediction of the measured value of 32,000 cm./hr. considering how vastly K can range (Table I) among typical stream gravels.

Most nebulous and difficult to measure of the variables required for calculating the permeability of a unigranular gravel is the shape Z. Heywood's method is too involved, requiring the use of a microscope on fine grains, to be practical

⁵A gravel which is a mixture of particles of all sizes is less porous than a unigranular gravel because the smaller grains fill the voids between the larger grains. The porosity of a unigranular material cannot be changed by compaction but depends solely upon the particle shape. The porosity of a bed of spheres of any one size, for instance, is invariably close to 0.40. Few natural materials, even unigranular materials of a jagged shape such as glass stucco, have a porosity exceeding that of a bed of uniform spheres. The high porosity of the pea gravel attests to its close grading about one size.

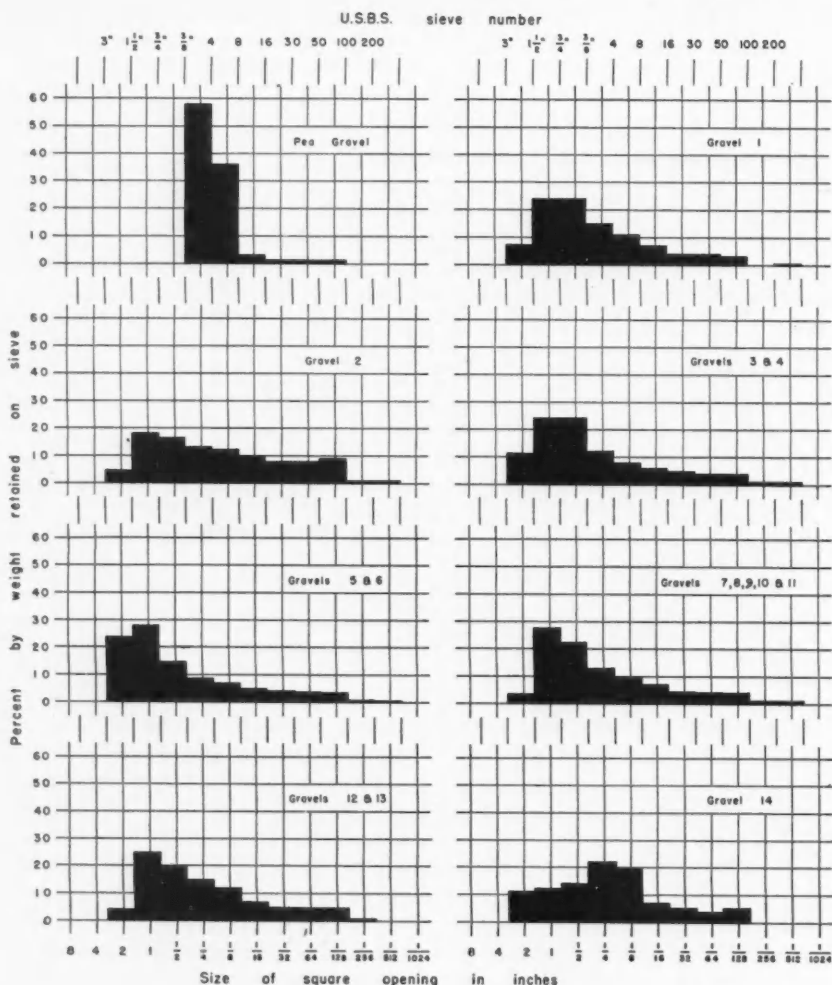


FIGURE 2. Grading curves of gravels listed in Table I.

in the field (assuming for the moment that stream gravels are unigranular). The shape of both a rounded and an angular spawning gravel was measured to ascertain the natural range in shape. Each size constituent of the two gravels was examined (Table II), the smaller sizes tending to be more jagged because the small particles are presumably younger than the larger ones. For the rounded gravel, Z measured 8.4, and hence a bed of this gravel would be 2.0 times as resistant as a bed of spheres. For the angular gravel, derived from weathered granite which fractured easily, Z measured 9.2, and hence a bed of it would be

2.4 times as resistant as a bed of spheres. Thus there is a range of but twenty per cent in permeability of spawning gravels due to shape alone, which is negligible in view of the vast range of K , and the shape factor $\left(\frac{Z}{6}\right)^2$ in Equation 9 could without appreciable error be taken as 2.0.

TABLE II. Calculation by Heywood's method of the shape Z of a rounded and an angular stream gravel. Five particles of each size were measured.

ROUNDED GRAVEL (Gravel 1)												
Sieve		Percentage retained	d	n	m	Shape	k _e	c	k	Z = $\frac{f'}{k}$	Z times conc.	
No.	Opening	by wt.										
	mm.	%	mm.									
1½-in.	38.1	7	53	1.3	1.5	Rounded	0.54	2.1	0.32	8.0	0.56	
¾-in.	19.1	24	33	1.3	1.4	"	0.54	2.1	0.34	7.8	1.87	
½-in.	9.52	24	15	1.4	1.5	"	0.54	2.1	0.36	7.3	1.75	
4	4.76	15	9.5	1.5	1.5	"	0.54	2.1	0.29	8.4	1.26	
8	2.38	11	4.9	1.7	1.7	Sub-angular	0.51	2.6	0.23	10.4	1.14	
16	1.19	7	1.6	1.6	1.5	"	0.51	2.6	0.27	9.6	0.67	
30	0.59	4	1.1	1.5	1.5	"	0.51	2.6	0.28	9.4	0.38	
50	0.297	4	0.58	1.4	2.0	"	0.51	2.6	0.22	10.6	0.42	
100	0.149	3	0.31	1.4	1.4	"	0.51	2.6	0.31	8.8	0.26	
200	0.074	0	0.16	1.2	2.0	"	0.51	2.6	0.23	10.0	0.10	
Pan		1	0.08-0.007			Angular	0.38	3.2				
Weighted mean										Z = 9.2		
ANGULAR GRAVEL												
Sieve		Percentage retained	d	n	m	Shape	k _e	c	k	f'	Z = $\frac{f'}{k}$	Z times conc.
No.	Opening	by wt.										
	mm.	%	mm.									
1½-in.	38.1	9	50	1.3	1.8	Rounded	0.54	2.1	0.26	2.3	8.9	.80
¾-in.	19.1	21	34	1.4	1.5	"	0.54	2.1	0.30	2.5	8.2	1.72
½-in.	9.52	27	21	1.3	2.0	"	0.54	2.1	0.24	2.2	9.4	2.54
4	4.76	11	7.6	1.3	1.6	Sub-angular to angular	0.51	2.6	0.28	2.6	9.3	1.02
8	2.38	9	3.2	1.2	1.7	Sub-angular	0.51	2.6	0.27	2.5	9.2	.83
16	1.19	9	2.3	1.5	1.2	"	0.51	2.6	0.30	2.5	8.5	.77
30	0.59	9	1.2	1.9	1.3	Sub-angular to angular	0.51	2.6	0.29	2.7	9.5	.86
50	0.297	4	0.73	1.8	1.7	Angular -various	0.4	3.1	0.18	2.3	13.0	.52
100	0.149	1	0.36	1.2	2.4	Angular -tetrahedral	0.38	3.2	0.15	2.0	13.9	.14
200	0.074		0.16			Angular -various	0.4	3.1				
Pan			<0.13			"	0.4	3.1				
Weighted mean										Z = 9.2		

d mean projected diameter of particles.

n length ratio (length/breadth) of particles.

m flatness ratio (breadth/thickness) of particles.

k_e volume constant for equidimensional particles.

k volume constant combining length, breadth and thickness.

f' surface coefficient of bed material

c a coefficient defined by the relation

$$f' = 1.57 + \frac{(n+1)ck^{1/3}}{n^{1/3}}$$

by Heywood's criticism of Rose (1954)

However, until someone discovers a significant way of expressing the size distribution U , we cannot calculate the permeability of a random gravel from the physical properties of gravel and water. The only way of determining the permeability of a redd is by measurement.

MEASUREMENT OF PERMEABILITY

DIRECT MEASUREMENT OF PERMEABILITY IN A PERMEAMETER

It follows from the definition that the permeability of a gravel can be measured simply by forcing water through a sample of it. A permeameter is a container for a sample of granular material which is equipped to show the head loss across a prism of the material when a liquid is forced through it.

The most usual design for a permeameter is a vertical cylindrical tank, with Bourdon gauges tapped into the wall at top and bottom. The tank is filled with granular material and liquid is pumped through it at a steady rate either upward or downward; the discharge is collected, timed and weighed; the pressure drop between the gauges is noted; and from these data the permeability is computed.

If Q is the volume rate of discharge, A is the cross-sectional area of the cylinder, Δp is the pressure drop in the length L of the cylinder, and ρg is the unit weight of the liquid, then the permeability is

$$K = \frac{V}{S} = \frac{\frac{Q}{A}}{\frac{\Delta p}{\rho g L}} \quad (10)$$

Another permeameter is a horizontal rectangular trough (Fig. 3) with two screens near each end to hold the sample, and a liquid-level recorder at each end to show the head loss over the length of the prism of granular material when liquid flows through it. The trough is filled between the screens with granular material; the liquid flows under gravity from a head pool at the upstream end to a tail pool at the downstream end, whose levels are held steady; the elevation difference between the head and tail pools is the head loss; the discharge into the tail pool is collected, timed and weighed; and from these data the permeability is computed. If V is the volume rate of discharge, A is the wetted cross-sectional area of the trough in mid-length, Δh is the head loss in the length between the screens, then the permeability is

$$K = \frac{V}{S} = \frac{\frac{Q}{A}}{\frac{\Delta h}{L}} \quad (11)$$

The permeability of a stream gravel can be adequately measured in a permeameter, either the tank or trough type. However, in transplanting the gravel from stream to permeameter, its degree of compaction will have been changed and hence its permeability, which according to Equation 9 is proportional to the fourth power of the porosity, and the permeability measured is no longer that of the stream bed.

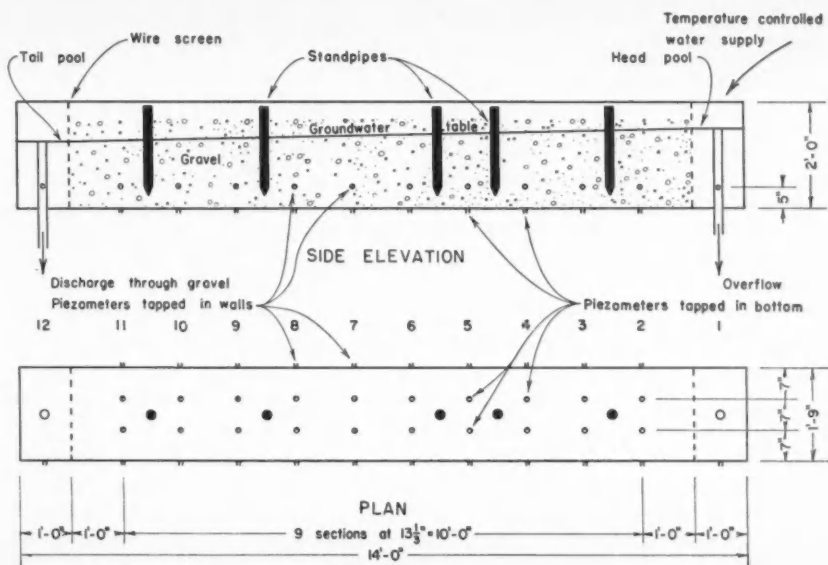


FIGURE 3. Drawing of trough-type permeameter used in laboratory and photograph showing standpipes being calibrated in trough full of gravel.

INDIRECT MEASUREMENT OF PERMEABILITY IN A WELL

The permeability of a bed of granular material can be measured indirectly by pumping a liquid out of, or into, a well drilled in the bed. If the geometry of the well and the dimensions of the bed are simple, by measuring the rate of pumping required to deliver the liquid to the given point in the bed at a steady rate under a known head, the permeability of the granular material can often be calculated by means of potential theory. Muskat (1937) shows how the permeability of shales to the flow of petroleum is determined by drilling and pumping. Johnson, Frevert and Evans (1952) show a method of measuring the permeability of soil to water by measuring the rate of inflow into an auger hole which has been pumped dry.

If we pump water from a known point P in a stream bed, then, assuming the existence of an impermeable stratum some distance below P, if the pressure head at P is reduced by some amount δh the position of point P in the bed, the permeability K of the gravel and the temperature govern the rate at which groundwater will converge on P. Thus K is a function of the suction head δh , the dimensions shown in Figure 4, and the steady rate of pumping q at temperature T.

$$K = f(\delta h, h_1, h_2 - h_1, q, T) \quad (12)$$

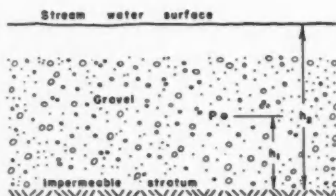


FIGURE 4. Critical dimensions governing groundwater flow into well at point P in stream bed.

A practical way of exhuming water from point P in the stream bed is through a standpipe. If the standpipe is always driven to the same depth in the gravel, dimension $(h_2 - h_1)$ is constant. Nor does the depth of the impermeable stratum affect the inflow to the standpipe provided dimension h_1 far exceeds the dimensions of the cavity at P. (van Bavel and Kirkham, 1948). Furthermore, if an arbitrary suction head is selected and always used, δh also is constant. By stipulating these standards, the unknown function has been simplified to

$$K = f(q, T) \quad (13)$$

which function may be determined by experiment in the laboratory. Thus the permeability of a stream bed *in situ* can be found by pumping water out of a standpipe driven into the gravel, measuring the rate of influx to the standpipe and reading the permeability from a calibration curve. This is the method adopted.

THE STANDPIPE

The standpipe (Fig. 1) is an artifice for creating, with a minimum disturbance of the gravel, a cavity ten inches below the surface of a stream bed, roughly the depth salmon lay their eggs. The hydraulic resistance of the holes in the chamber must be low compared with the pores in the most permeable gravel so that the rate of influx will be governed by the gravel. Nevertheless the holes must be tiny enough to exclude sand from the chamber. The shank of the standpipe is an adit to the chamber at the bottom; its bore is just large enough to admit a thermometer and sampling tube.

The standpipe is driven to the prescribed depth vertically into the stream bed where the rate of oxygen supply is sought. Groundwater is pumped out of the standpipe at the steady rate which maintains the water level in the shank exactly one inch below the surface stream level. This steady rate of discharge q is measured and the groundwater temperature in the standpipe is noted. The permeability K of the gravel at the observed temperature is read from the calibration curve (Fig. 5) of q against K determined in the laboratory, where the permeameter (Fig. 3) was used as a standard or model stream bed.

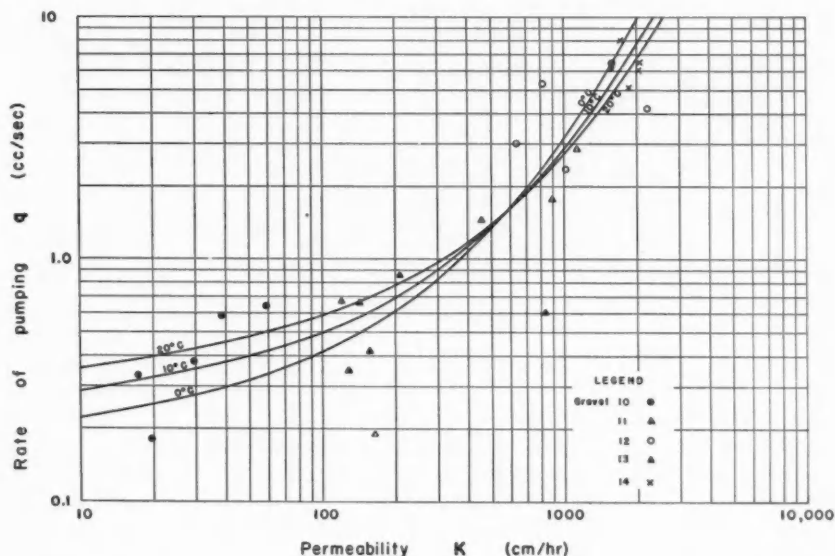


FIGURE 5. Calibration curves of rate of pumping groundwater from standpipe under one-inch suction head against permeability of gravel at temperatures 0°C., 10°C., and 20°C.

MEASUREMENT OF THE HYDRAULIC GRADIENT IN A STREAM BED

It is assumed that both the groundwater and the surface flows of a stream are *steady*. The groundwater flow will not be *uniform* unless the gravel happens to be uniformly resistant throughout, which is unlikely. The pressure head at

any point within a saturated stream bed is the height above that point to which a column of water would rise in a vertical piezometer tube. If the groundwater and surface flows were each uniform the water level in the piezometer would coincide with the surface water level and the hydraulic gradient would be the slope of the surface water. As a crude approximation, the hydraulic gradient could be read off a contour map. Better, the free-surface slope could be measured over a short reach of the stream by measuring the water level difference between two stilling wells.

We can readily see if the surface flow over a particular short reach of a stream is uniform, but we cannot tell whether the groundwater seepage is uniform; in fact, there would be no reason to suppose it was unless we knew the bed to be composed of an especially homogeneous mixture of particles of uniform size, roughness and shape. Therefore we should try to measure the groundwater hydraulic gradient proper, rather than accept the free-surface slope.

One possible way is to bury the ends of a sensitive two-fluid multiplying manometer into the stream bed at either end of the reach over which we wish to know the gradient. The manometer measures the difference in groundwater pressure between the points of burial. Digging, however, where the ends of the manometer are to be buried alters the hydraulics of the gravel.

INDIRECT MEASUREMENT OF HYDRAULIC GRADIENT IN A WELL

The most convenient method of measuring the hydraulic gradient, and the one adopted, is in a well—by means of the standpipe. The groundwater flows into the holes on one side of the standpipe and out the other side at a rate depending on the pressure difference across the standpipe, and hence upon the hydraulic gradient. Tests have shown that the flow through these orifices is laminar, and therefore the absolute velocity v through each orifice is proportional to the gradient S in the gravel near the standpipe. Since the orifices are symmetrically arranged around the chamber, the direction of the groundwater flow does not affect the volume rate of exchange α in the chamber, which is proportional to v and hence also to S . The hydraulic gradient is measured by dropping some dye into the standpipe and observing how quickly it fades; the faster the dye is diluted, the steeper is the gradient. It follows that the rate of dye dilution is a function of the gradient, provided the flow through both the gravel and orifices is laminar, regardless of the physical properties of the gravel into which the standpipe is driven. Experiment supports this supposition. This method has the advantage of measuring the gradient over a reach of the stream so short—the width of the standpipe—as to be considered a point.

MECHANISM OF DYE DILUTION IN THE STANDPIPE

Assuming that the dye solution in the chamber is instantaneously mixed with the clear diluent as soon as it enters, at any instant the dye concentration

$$C = C_0(1 - \alpha)^t \quad (14)$$

where C_0 is the initial concentration, t is the time interval since dilution started, and α is the fraction of the volume of the chamber exchanged per unit time.



FIGURE 6. Dye solution being pipetted into standpipe for measuring the hydraulic gradient.

The rate at which the dye is diluted in the chamber is measured as follows. About 5 ml. of 1% methylene blue dye solution is pipetted into the top of the standpipe (Fig. 6) and is mixed with the water inside. A sample of this mixture is withdrawn immediately and its opacity measured by visual comparison with a rack of standards (Fig. 7). The standard dyes are arranged in decreasing concentrations in a geometric series having common ratio r . Each tube is labelled with a natural number n , called an opacity number, in an arithmetic series. Thus the concentration of the dye in any tube numbered n is given by

$$C = C_0 r^{n-1} \quad (15)$$

where C_0 is the concentration of the dye in the first tube, numbered 1. After any convenient time another sample is withdrawn for an opacity measurement. The rate of dye dilution is expressed as the difference between the initial and final opacity numbers divided by the time interval between the two observations.

Equating (14) and (15),

$$(1-\alpha)^t = r^{n-1}. \quad (16)$$

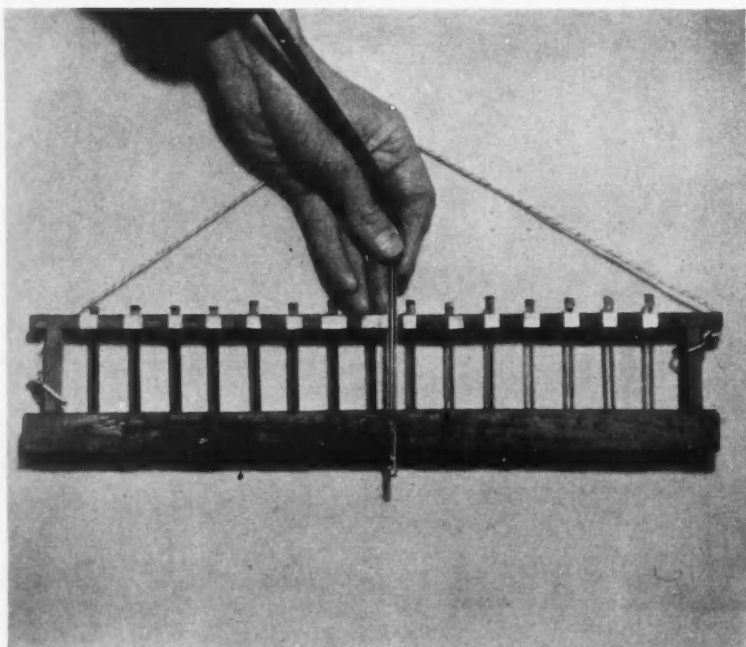


FIGURE 7. Measuring the opacity of a sample of dye from the standpipe by visual comparison with a rack of standard concentrations.

Differentiating (16)

$$\frac{\partial n}{\partial t} = \frac{\ln(1-\alpha)}{\ln r}. \quad (17)$$

Equation 17 shows that, for a given rate of exchange α , and hence for a given seepage velocity V or gradient S , the rate of change of opacity number $\frac{\partial n}{\partial t}$, called the *rate of dye dilution*, is constant and independent of the initial concentration C_0 or the time interval t between observations. This means that if the mechanism of dilution in the standpipe is actually like that which was assumed, the change in opacity number with time can be expressed as a family of straight lines, each passing through the origin, and the slope of each increasing with increasing values of the parameter S . Obviously the greater the rate of exchange α , and hence the steeper the gradient S , the faster is the change in opacity number. Experiment shows (Fig. 8) that, with stirring every 15 minutes, the rate of dye dilution is in fact fairly constant.

Differentiating (17), the rate of change of $\frac{\partial n}{\partial t}$ with changing α

$$\frac{\partial}{\partial \alpha} \left(\frac{\partial n}{\partial t} \right) = -\frac{1}{\ln r} \left(\frac{1}{1-\alpha} \right), \quad (18)$$

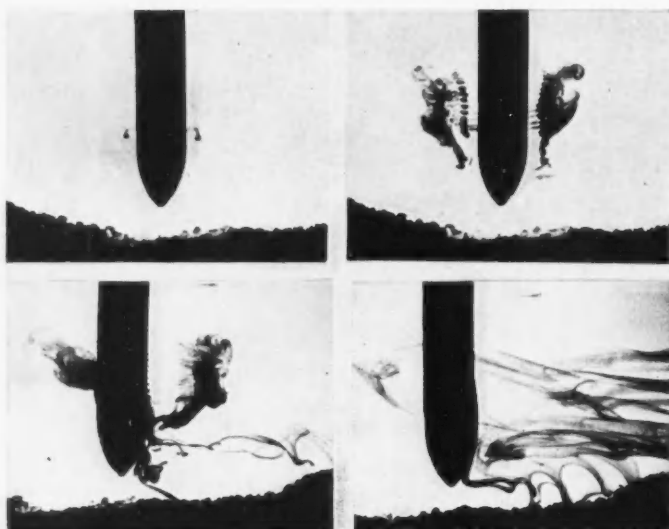


FIGURE 9. Photographs of dye lost from standpipe in aquarium of water due to stirring and to density difference between dye solution and clear water. TOP ROW (water still): *Left*, dye exuded after first plunge of sampling tube; *right*, dye exuded after second plunge. BOTTOM ROW (water flowing): *Left*, dye exuded after second plunge; *right*, dye ten minutes after completion of third successive plunge. Note dye oozing out of downstream holes in chamber as a result of density difference.

water level in the shank. Now the thumb is lifted and the mixture falls out of the tube onto the mixture in the shank. This procedure is repeated three times in quick succession, the third tubefull being used for the opacity measurement, after which the sample is returned to the standpipe. This stirring technique displaces the denser dye solution from the bottom of the chamber to the water surface in the shank.

A standpipe was tested in a glass aquarium full of water without gravel to see what happened during the dye injection and the subsequent stirring (Fig. 9). No dye exuded from the holes while the pipette was draining; immediately after, the dye lay unevenly mixed in the shank; thereafter, if stirring was delayed, it sank into the chamber, and, later still, oozed out of the holes, even in the absence of a flow through the aquarium. When the mixture was stirred the dye solution in the chamber spurted out through the holes each time the tube was plunged. There being no appreciable mixing forces outside the standpipe, the puffs of dye and the ambient clear water retained their identity; since the dye solution was the denser, it settled slowly through the clear water. Presumably, when gravel surrounds the standpipe, a smaller volume of dye solution is expelled from the chamber by plunging the tube than when the standpipe was tested in clear water, because there now exists a large hydraulic resistance outside the holes which the unbalanced head inside the standpipe has not time to fully

overcome before the unbalance itself is reversed by the withdrawal of the tube above the water surface in the shank. Presumably, also, the gravel contains what dye solution does exude from the chamber during stirring in the immediate environ of the holes, so that each time the tube is raised some of the escapement homes.

The following stirring schedule was adopted:

Step 1—Injection	{ Drain pipette into standpipe	9 seconds
	{ Wait	3 to 5 seconds
	{ Remove pipette	2 seconds
	{ Delay	6 to 12 seconds
Step 2—Mixing (Repeat once)	{ Lower tube closed	4 seconds
	{ Open tube and close again	1 second
	{ Raise tube closed	1 second
	{ Open tube and close again	2 seconds
Step 3—Sampling	{ Lower tube closed	4 seconds
	{ Open tube and close again	1 second
	{ Raise tube closed	1 second
	{ Opacity	10 to 25 seconds
	{ Open tube	1 second

The total time required for the whole program above is from 50 to 80 seconds. The first step introduces a slug of dye into the standpipe, the second mixes the dye with the water in the standpipe, and the third measures the opacity of the resultant dye solution in the standpipe. This gives us an initial opacity at time zero.

Now let us see what happens to the dye solution in the chamber after time zero. The aquarium test revealed that the flow through the chamber is minute and definitely laminar, the clear groundwater intruding in threads which do not mix with the dye solution in the chamber. This water floats to the surface of the dye solution in the standpipe with the result that as time progresses the liquid inside the chamber becomes stratified, clear water or light-coloured dye solution lying at the top and concentrated dye solution lying at the bottom with a gradual transition in colour between.

As a result of this tendency to stratify, it is necessary to again stir the mixture in the chamber to an even colour before withdrawing a sample for the second opacity measurement. So steps 2 and 3 of the stirring procedure are repeated every 15 minutes after time zero for one hour or until the dye becomes too dilute to measure the opacity.

Equation 17 dictates that the rate of dye dilution is a constant for a given gradient. Accordingly, straight lines have been imposed upon the experimental points (Fig. 8) of total dilution against time with the standpipe in a typical spawning gravel. It is frequently apparent that a curve, not a straight line, would better fit the points, though the discrepancy is slight. The typical curve (Fig. 10) indicates that the rate of dilution is somewhat faster at first and

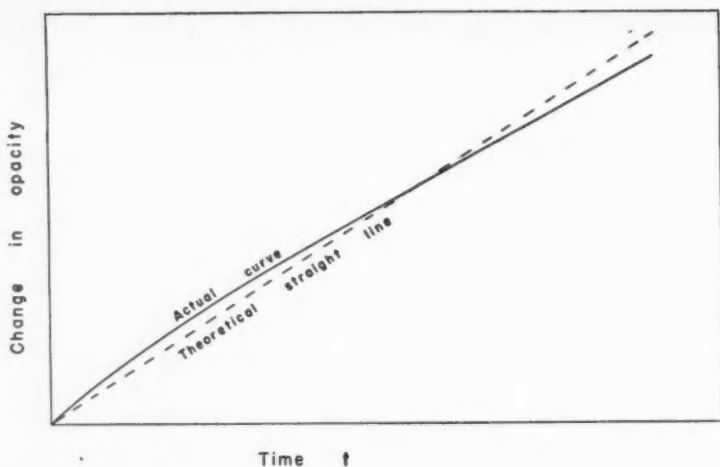


FIGURE 10. Typical plot of total change in opacity number against time after introduction of dye to standpipe, at any particular gradient, illustrating deviation from Equation 17 owing to density difference between dye solution and clear water.

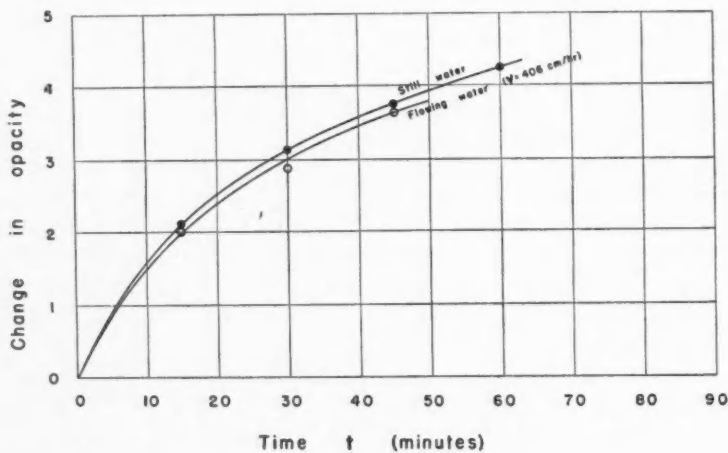


FIGURE 11. Plot of total change in opacity number against time after introduction of dye to standpipe in aquarium of water, showing dye loss by stirring and density difference between dye solution and clear water.

decreases to attain a constant value, the reason being that the dye which weeps out of the holes in the chamber because of density difference weeps faster at first, when the density difference between the dye solution in the chamber and the water outside is greater.⁶

Proof of this explanation is the rate of dye dilution curves observed with the standpipe in an aquarium of water without gravel (Fig. 11). (Note that the curves for flowing and still water were nearly coincident because the gradient was immeasurably flat, corroborating the theory that the dye dilution measures gradient regardless of velocity.) The dye dilution observed was due solely to stirring and to density difference. The curve is the sum of two effects, first, a straight line due to the constant loss of dye by stirring and, second, a curve due to the loss of dye by density difference, which decreases with time. It is logical to suppose that both these effects taint the rate of dye dilution when the standpipe is in gravel; the loss by stirring is responsible for the observed rate of dilution at zero gradient, or still water, shown in Figure 8, and the loss by density difference causes the observed departure from Equation 17 depicted in Figure 10.

LABORATORY INVESTIGATION OF TYPICAL SPAWNING GRAVELS

In the laboratory, one uniform gravel and 14 random stream gravels (Table I) were tested in an open-trough permeameter. The gradation of the grains, the porosity and the permeability of each experimental gravel bed were measured.

MECHANICAL ANALYSIS OF GRAVELS

A nest of eleven sieves (Table III) was used to separate samples of each gravel into twelve size ranges. The sieves were U.S. standard series sieves, with square openings, each twice as large as the next smaller, and were mechanically shaken to ASTM specifications. The percentage of the sample retained in each sieve was plotted against the logarithm of the size (Fig. 2).

TABLE III. Sieves used to measure the gradation of the gravel grains.

Mesh No.	Square opening
	<i>inches</i>
3	3.00
4	1.50
10	0.750
20	0.375
40	0.187
80	0.0937
160	0.0469
320	0.0232
640	0.0117
1280	0.0059
2560	0.0029

⁶Such weeping could be minimized by starting with an infinitely dilute dye solution, whose specific gravity almost equalled unity. But the concentration of so weak a dye could never be measured colorimetrically. A salt and electric method would be preferable because salinity can be measured most accurately at low concentrations, but requires the measurement of both temperature and salinity with delicate equipment.

THE PERMEAMETER

An open-trough permeameter (Fig. 3) was used to measure the permeability of the gravels. It was effectively an artificial stream complete with gravel bed through which either a groundwater flow only, or both a groundwater and a surface flow could be set. The inside was stuccoed with sand to prevent water slipping along the walls instead of percolating through the gravel.

A flow was induced through the gravel by depressing the overflow pipe in the tailwater pool slightly below the level of the overflow pipe in the headwater pool, and held steady by supplying water to the headwater pool faster than the discharge through the gravel. The seepage velocity was varied by altering the height of either overflow pipe.

The apparent velocity was measured by catching and weighing the discharge from the tail pool overflow pipe over a timed interval, computing the volume rate of discharge and dividing this by the width of the trough times the depth of groundwater.

The water used in the experiments was temperature controlled. Hot and cold water from the laboratory supply were mixed to the desired temperature before flowing into the headwater pool.

Piezometers in the sides and bottom of the trough showed the pressure head of the groundwater at the points in the gravel bed where the trough had been tapped. The piezometer scales referred to the level of the bottom of the trough and could be read within plus or minus 0.01 inch.

From each of the gravels tested in the trough the following data were gathered:

1. The gradation of the grains
2. The porosity of the gravel in the trough
3. Forty-two piezometer heights for each different flow
4. The apparent velocity in the middle of the trough for each flow
5. Eight temperatures—one each of the head pool, tail pool and room, and one in each of five standpipes driven into the gravel—for each flow.

MEASUREMENT OF POROSITY

The average porosity of a gravel bed *in situ* in the trough was measured by filling the trough with water almost to the surface of the gravel. The dimensions of the trough, the depth of the water and the weight of water added being known, the porosity was calculated as follows:

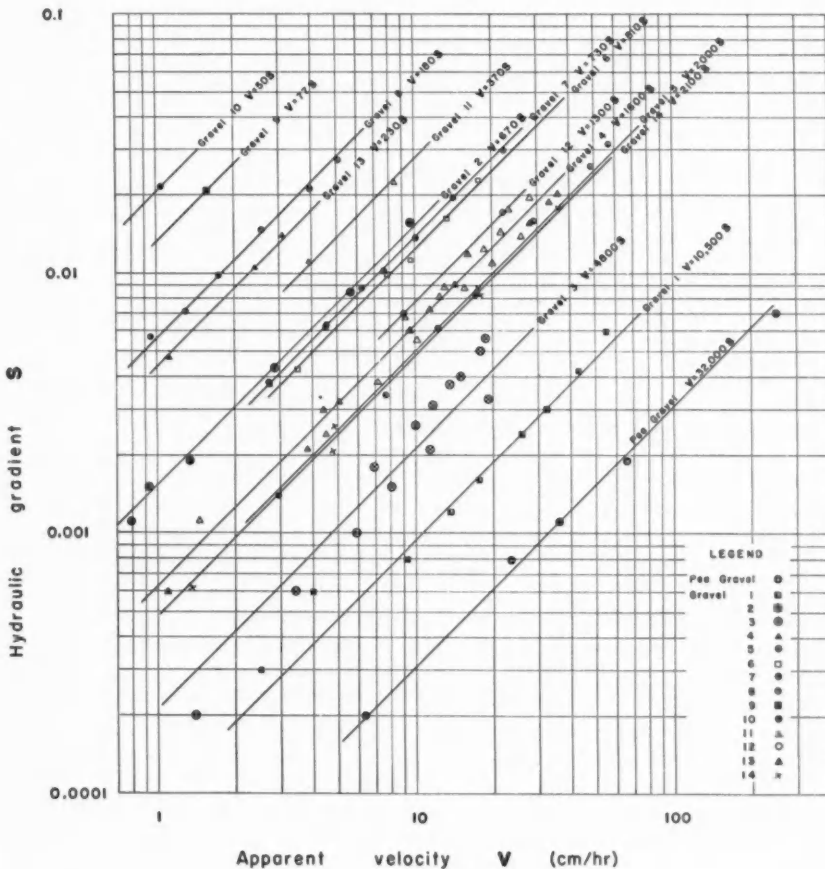
$$\text{Porosity} = \frac{\text{Volume of water}}{\text{Volume of water plus gravel}} \quad (20)$$

This procedure is precise only if the gravel is absolutely dry at the start, but to attempt to dry so large a volume of gravel as the trough holds, about one cubic yard, was an impractical task. We were forced to accept damp or even wet gravel, and therefore expected our values for porosity to be too low. Alternatively, the porosity was measured by draining and weighing the water from the trough full of gravel. This yielded an even lower value because the gravel was still wet after draining. The more compact the gravel, the less reliable was the value of

its porosity. Any accurate way of measuring the porosity involves drying the gravel.

EVIDENCE THAT DARCY'S LAW APPLIES TO A STREAM BED

The permeability of each of the gravels listed in Table I was measured in the trough at several seepage rates. The plots (Fig. 12) of average hydraulic gradient over the length of the trough against apparent velocity, corrected for temperature by Equation 21, show that the velocity is proportional to the gradient for every gravel, even the pea gravel, within the range of flows examined, and hence Darcy's Law applies. Since the gradients in a natural stream seldom would



exceed the steepest used in the laboratory and since we are not concerned with stream gravels more permeable than gravel 1, it is safe to say that Darcy's Law holds in most salmon redds.

EFFECT OF TEMPERATURE ON PERMEABILITY

Rose showed (Equation 9) that the permeability of a bed of spheres is inversely proportional to the kinematic viscosity $\frac{\mu}{\rho}$ of the fluid. Accordingly, in this work all velocities have been reduced to a common temperature of 10°C. by the following equation:

$$\text{Velocity at } 10^{\circ}\text{C.} = \text{Velocity at } T^{\circ}\text{C.} \frac{\text{Kinematic viscosity at } T^{\circ}\text{C.}}{\text{Kinematic viscosity at } 10^{\circ}\text{C.}} \quad (21)$$

DIFFERENCES IN PERMEABILITY WITH DIRECTION OF FLOW

Unless the particles are spherical there is no *a priori* reason to suppose that a bed of granular material will be equally permeable in all directions. A bed of

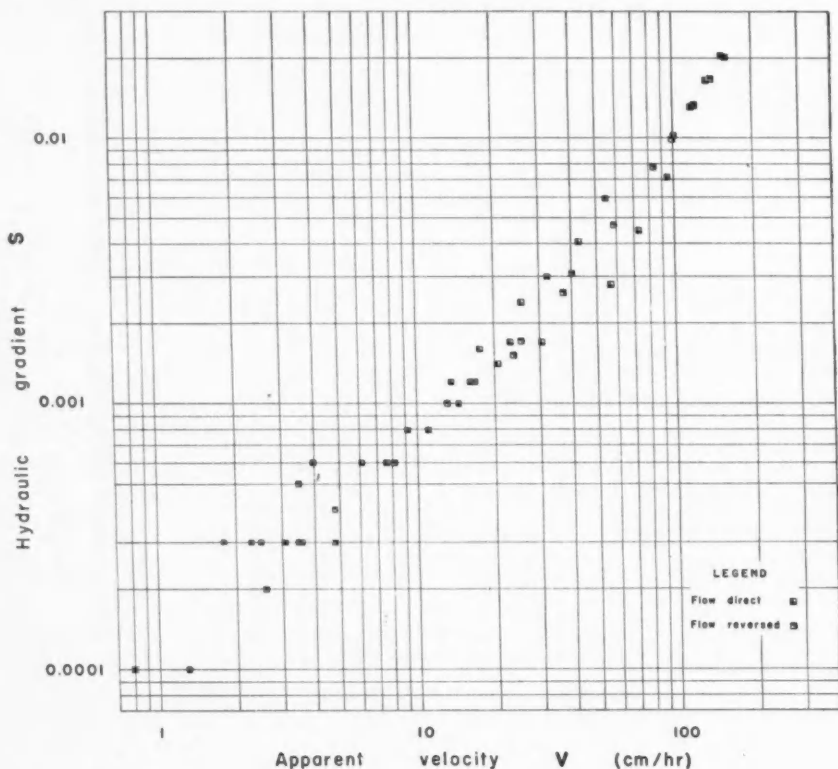


FIGURE 13. Log-log plot of average hydraulic gradient against apparent velocity, at 10°C., with direct and reversed flows in gravel 1.

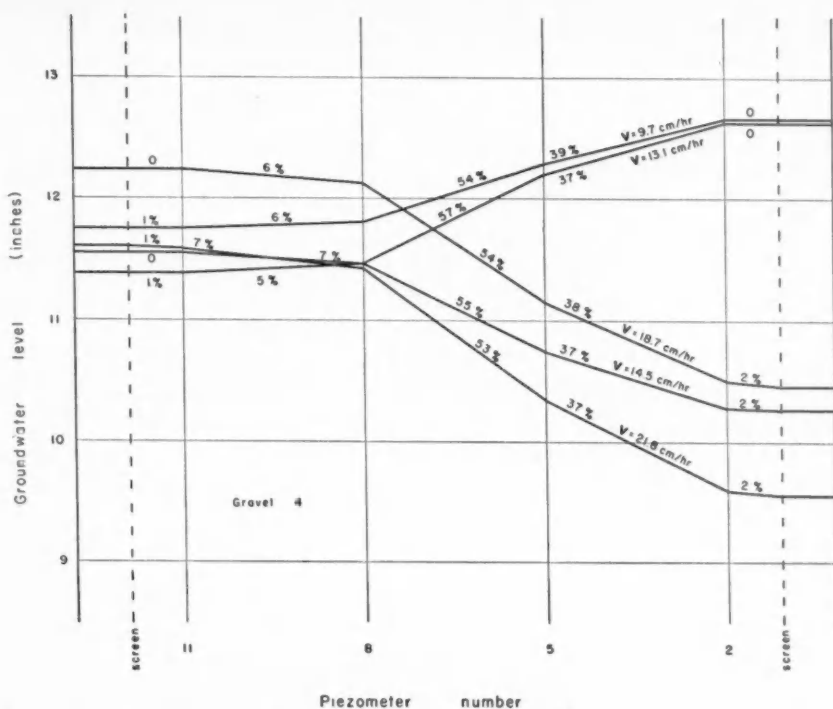


FIGURE 14. Pressure surface profiles in gravel 4, showing percentage of total lost head occurring between piezometers 1, 2, 5, 8, 11 and 12 is constant regardless of direction of flow.

non-spherical particles whose orientation is not completely random will have a permeability differing with direction. Such anisotropy is not to be confused with the permeability of a bed changing from point to point in one given direction owing to changes in porosity, a vagary which is discussed later.

Some evidence of the isotropy of a stream bed must be shown before the standpipe may justifiably be used to measure its permeability. Accordingly, water was forced through troughfills of typical stream gravel, first in one direction, then in the opposite, to see whether there was any difference in permeability between the two. Admittedly it would have been preferable to compare the permeabilities in three mutually orthogonal directions through a prism of gravel, but the equipment was lacking.

Figure 13 shows the plots of average gradient against apparent velocity in gravel 1, with the points for direct and reversed flow distinguished. Evidently the overall permeability of this bed is the same whether the flow be direct or reversed.

Figure 14 shows pressure surface profiles in gravel 4 for two direct and three reversed flows read from piezometers 40 inches apart in the left wall of the trough. It will be seen that the fraction of the total head loss occurring in any one of the 40-inch spans is the same regardless of the direction of flow.

PRESSURE SURFACE IN TROUGH FILLED WITH UNIGRANULAR GRAVEL

When water was run through the uniform pea gravel, the pressure surface indicated by the 42 piezometers (Fig. 15) was, within the limits of observation, a sloping surface, level across the trough and concave down longitudinally (Mavis and Tsui, 1939). It is concluded that when water flows through a random gravel in the trough, any undulation in the pressure surface is due to variations in permeability from point to point within the gravel.

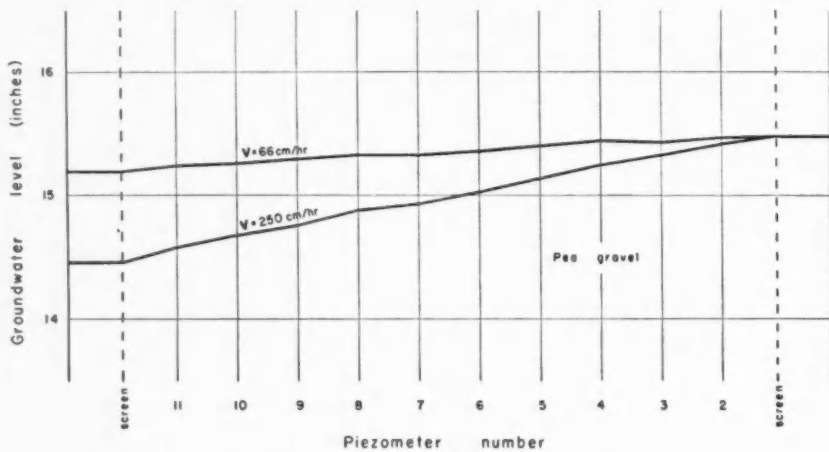


FIGURE 15. Pressure surface profiles in pea gravel, showing uniformity of slope.

PRESSURE SURFACE IN TROUGH FILLED WITH RANDOM GRAVEL

Despite every precaution taken to mix each random gravel uniformly and to compact it evenly in the trough so that the porosity and hence the permeability would be roughly constant everywhere throughout the bed, the pressure surface indicated by the piezometers was invariably an undulating one. In a few gravels the surface had a fairly uniform slope, but in most the surface slope frequently changed abruptly, revealing that the permeability of the gravel changed from point to point and that the groundwater flow, though steady, was not uniform throughout the bed.

Figure 16 shows contour plans of the pressure surface at the nominal apparent velocity 10 cm./hr. in gravels 14, 5 and 8. The contour interval is the same in each of the three plans. It is seen that the permeability of gravel 14 happens to be uniform throughout the bed, for the contours run at right angles to the trough and are equally spaced, whereas the permeability of gravel 5 is not uniform, for the contours are crooked and unequally spaced. Gravel beds 14 and 5 are approximately equally permeable and gravel bed 8 is more than ten times as resistant (Table I). The low permeability of gravel 8 is manifested in the tightly

packed contours, which also are crooked and unequally spaced. The uniform permeability of a random gravel, such as that of gravel 14, is the exception rather than the rule.

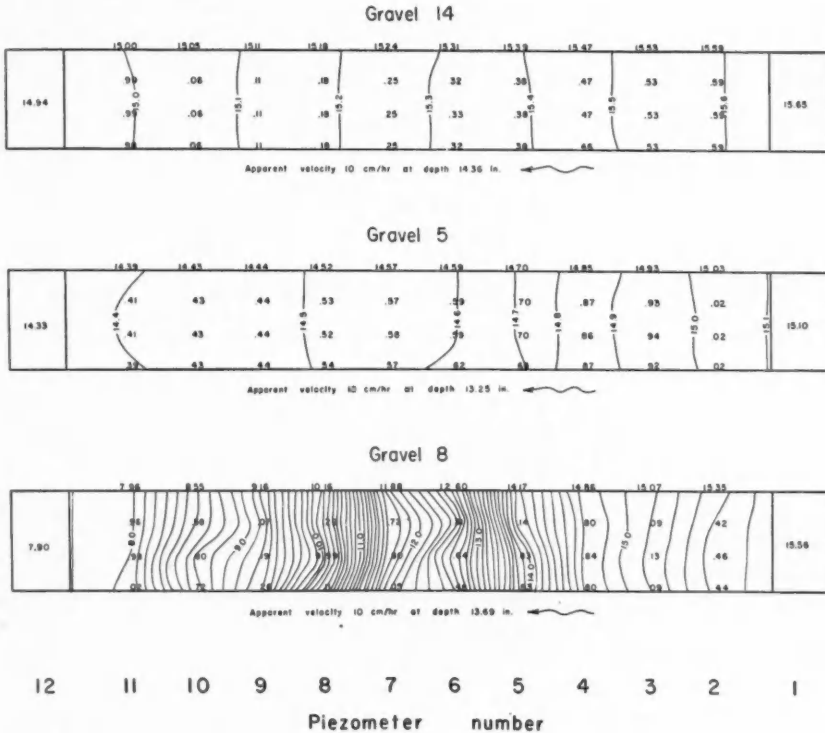


FIGURE 16. Contour plans of pressure surface in gravels 14, 5 and 8 at the nominal apparent velocity 10 cm./hr. Figures are piezometric heights in inches, with decimal point at plan position of piezometer.

VARIATION OF PERMEABILITY WITH POROSITY

Rose found (Equation 9) that the permeability of a bed of uniform spheres varies approximately as the fourth power of porosity. Mavis and Wilsey (1936) found that the permeability of a bed of rounded sand varies as the fifth power of porosity and of angular sand as the sixth. All the foregoing were measured at high values of porosity.

Gravels 7, 8, 9 and 10 (Table I) are composed of the same particles; they differ only in porosity, having been successively compacted by tamping. If we assume that the permeability K of a bed of random gravel is proportional to the average porosity p raised to some unknown exponent θ , then,

$$K \sim p^{\theta} \quad (22)$$

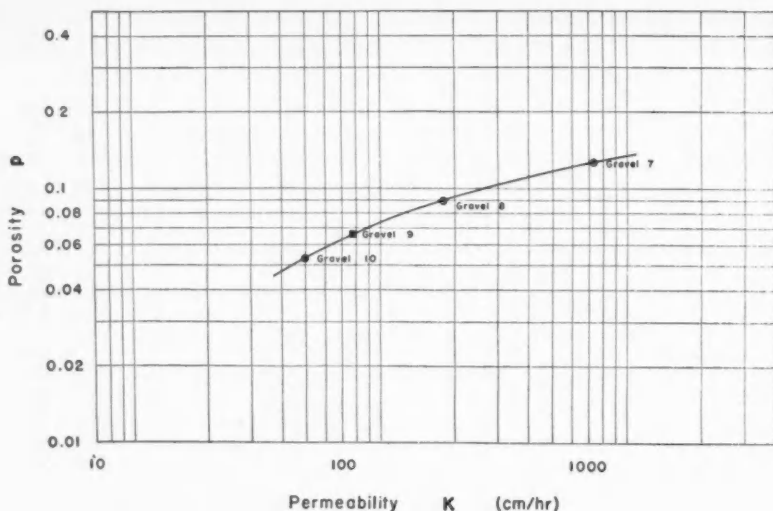


FIGURE 17. Log-log plot of permeability against porosity for one gravel bed successively compacted.

and the value of θ is the slope of the curve when $\log K$ is plotted against $\log p$. Figure 17 shows this curve for random-gravel beds 7, 8, 9 and 10. Evidently, since the points do not fall on a straight line, the exponent θ is not a constant; rather its value increases with porosity. For these compact gravels θ varies from 2.0 at porosity 5% to 4.0 at porosity 12%.

The profound variation of θ with p is shown in Figure 18, reproduced from

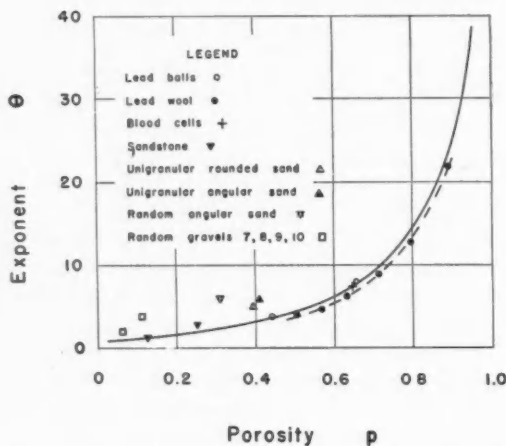


FIGURE 18. Variation of porosity p with exponent θ in Equation 22.

Rose. In order to determine the variation of the exponent θ over a range of porosities wider than is possible with uniform spheres, Rose tested lead wool. He plotted his results from spheres and lead wool together with Whittington's data on blood cells and Muskat's on sandstone (Fig. 18). Coincidence of the four is remarkable. We have added to this graph Mavis's (1936) random angular sand, unigranular angular sand and unigranular rounded sand, and our random gravel. That θ increases with p for any given material there is no doubt, but the relation seems to depend somewhat upon the shape of the material. It appears a curve of θ against p for river sand and gravel particles would lie slightly above Rose's curve for spheres.

It is concluded that, since it is practically impossible to measure the porosity p of a stream bed *in situ* and since furthermore the exponent θ varies not only profoundly with p but also slightly with shape, to calculate the permeability of the bed from the physical properties of gravel and water is even less feasible.

CALIBRATION OF STANDPIPE TO MEASURE PERMEABILITY

The head used in the permeability measurement must be low to ensure that the flow through the gravel toward the standpipe is laminar. Furthermore, if the head be too high, not only will the flow be turbulent but also the gravel fines may be physically moved by the flowing water, and the rate of influx into the standpipe no longer will be a measure of the natural permeability of the stream bed.

This "hydraulicking" was shown to occur by an experiment where water was poured into five standpipes driven in gravel 9 under successive constant heads of 4, 8, 4, 20 and 4 inches. The rate of dissipation of this water through the gravel was found to be steady. Table IV shows how the flow at 4-inch head had increased after the gravel had been subjected to the 8-inch head, and increased again after the 20-inch head. Evidently the high heads had "hydraulicked" an easier path of escape to the surface for the water flowing down the standpipe than through the original natural pores in the gravel.

Theoretically, the permeability of a stream bed can be measured equally well by pumping water either out of or into a standpipe provided the head is low. The alternative of "pumping-out" was adopted because the prescribed low head could be more accurately maintained.

TABLE IV. Rate of discharge from five standpipes in gravel 9 at successive 4-inch heads, showing increase following "hydraulicking" under higher heads.

Constant heads in order of succession	Steady rate of discharge into standpipe (unspecified units)				
	1	2	3	4	5
<i>inches</i>					
4	175	91	87	193	193
4	184	100	89	229	219
8	375	225	185	440	398
4	243	153	116	275	245
20	812	410	404	685	832
4	286	167	139	316	341

Five standpipes were calibrated in the trough (Fig. 3) in each of gravels 10, 11, 12, 13 and 14 for rate of pumping, with water entering the chamber under a one-inch head, against permeability. Both the apparent velocity used to compute the permeability and the rate of pumping were reduced to the common temperature 10°C. by Equation 21.

The permeability value tributary to each standpipe was computed, for want of better data, from the slope of the pressure surface given by the piezometers straddling the standpipe. For example, from the contours (Fig. 16) the gradient in the vicinity of a standpipe driven in gravel 8 between sections 5 and 6 is 0.113, and the apparent velocity at depth 13.2 in. at 10°C. is 10.3 cm./hr., whence the permeability is $\frac{10.3}{0.113} = 91.3$ cm./hr. This value of K would be plotted against the observed rate of pumping q at 10°C. of 0.47 cc./sec. in compiling the 10°C. calibration curve (Fig. 5). The 0°C. and 20°C. curves are calculated from the 10°C. curve.

The scatter of the points is attributed to the variation in permeability from point to point within the gravel. If each of the five gravels had been homogeneous in permeability then the calibration graph would contain five sets of tightly grouped points, like the points for gravel 14.

CALIBRATION OF STANDPIPE TO MEASURE HYDRAULIC GRADIENT

Five standpipes were calibrated in the trough (Fig. 3) in each of gravels 5, 6, 7 and 8 for rate of dye dilution against gradient. For several seepage rates through each gravel, the dye concentration was observed in each of the five standpipes at 15-minute intervals. The change in opacity number in each standpipe was plotted against time for each flow in each gravel. Straight lines were imposed on these points (Fig. 8) in accordance with Equation 17. The slope of one such line is the ordinate of a point on the calibration graph of dilution against gradient (Fig. 19).

Even when the groundwater is still, the dye fades in the standpipe. This zero flow rate of dilution, or *zero dilution*, caused by dye weeping from the holes in the chamber and by stirring, is practically a constant regardless of the properties of the gravel, about 1.5 opacity number per hour.

For each of the four gravels a best straight line has been drawn through the points on the graph of dilution against gradient with two restrictions imposed, namely, that the line pass through the average of the zero dilutions, and that it be straight according to Equation 19.

The slope of the four lines seems to be governed by neither the gradation of the grains, the permeability nor the porosity, but rather by the degree of compaction of the gravel (Table I). Regardless of the physical properties of the gravel, the slope of the calibration line is about 6.5 opacity number per hour per 0.01 gradient if the gravel is loose, and about 3.3 if the gravel is compacted as tightly as that particular gravel can be. Since these four gravels encompass so large a permeability range among typical stream gravels (Fig. 12), and since streams usually lay their beds compacted, one calibration line drawn through

zero dilution 1.5 and having slope 4 is considered adequate for finding the gradient in any spawning gravel, in view of the wide scatter of the experimental points.

The scatter of the points in Figure 12 stems largely from our inability to measure the precise value of the gradient in the vicinity of the standpipe in the

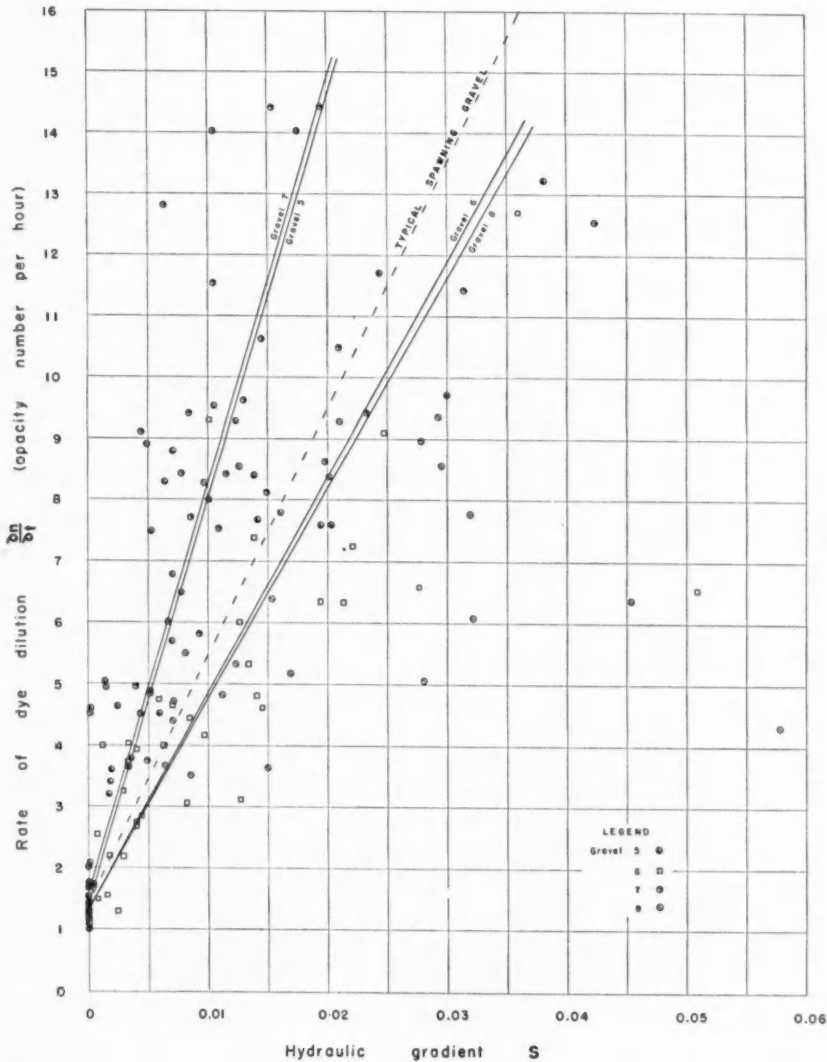


FIGURE 19. Graphs of rate of dye dilution against hydraulic gradient in gravels 5, 6, 7 and 8, with accepted calibration line for any spawning gravel.

trough. It is the pressure drop across the chamber which determines the rate of dilution, yet, for lack of closer information, we assume that the gradient in the vicinity of the standpipe equals the average gradient indicated by piezometers 13 1/3 inches apart. In the field, therefore, a single value never should be accepted; rather, at least three standpipes should be driven in the same redd to give a more statistically significant value of the gradient.

FIELD PROCEDURE

The equipment designed to measure the oxygen supply to a redd weighs about thirty pounds and consists of:

1. A standpipe⁷ complete with driving cap, extension tube and disc (Fig. 1) and 2-lb. hammer.
2. The suction gear for measuring permeability, namely, a bicycle pump, graduated flask, light rubber hose, stainless-steel tube with sliding marker, thermometer and stopwatch (Fig. 20).

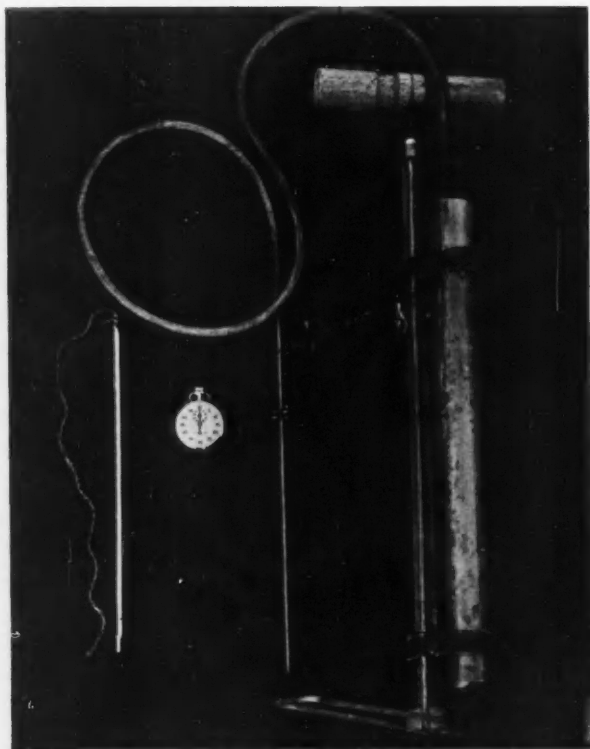


FIGURE 20. Photograph of suction gear used to measure permeability.

⁷A detailed shop drawing of the standpipe may be obtained by writing to the Director, Pacific Biological Station, Nanaimo, B.C.

3. A portable Winkler kit for measuring the oxygen concentration (Harper, 1953).

4. A bottle of 1% methylene blue dye for measuring gradient, with stirring tube and rack of standards (Fig. 7).

5. The calibration curves determined in the laboratory of pumping rate with permeability (Fig. 5) and of rate of dye dilution with gradient (Fig. 19).

The following procedure is suggested for measuring the oxygen supply to a redd:

1. With the cap screwed on snugly, drive the standpipe with a 2-lb. hammer vertically into the stream bed where the rate of oxygen supply is sought until the red band lies flush with the top of the gravel. The cap threads are parallel in order that the hammer blows may be transmitted to the hard point via the flat top of the standpipe. Remove the driving cap. The standpipe is designed for use alone in streams where the surface water is up to 6 inches deep; in deeper water drive the standpipe to the same mark, by means of a follower underwater and, after removing the cap, screw on the extension tube. The open top of the standpipe or its extension must lie clear above the surface water with some free-board. All this should be done with the least possible disturbance to the stream bed; in driving, the standpipe should be struck axial blows; prying the gravel by inadvertent lateral forces on the top of the standpipe should be avoided; nor should the standpipe be twisted when the cap is unscrewed or the extension added. Next, scrape away the top inch of gravel from an 8-inch circle around the standpipe and replace it with the finest sand at hand which the current will not wash away. Then slip the brass disc over the standpipe and press it firmly down upon the sand. The purpose of this disc is to prevent water from slipping down the outside wall of the standpipe and thence into the chamber when water is being pumped out of the top of the standpipe. Only occasionally is the pumping rate different with and without the disc. Therefore, since weight counts, the biologist might decide to omit the disc from his equipment at the risk of getting a few permeability values which are erroneously high.

2. First of the three quantities measured is the permeability. The plunger on the pump is changed to suck air instead of to pump. The flask serves both as a vacuum tank and as a measure. An assistant is needed here to work the pump and hold the flask. The water level inside the standpipe is first located by pushing the steel tube down into the shank, sucking all the while, until the first "slurp" is heard. The tube is then withdrawn and the sliding marker, which now indicates the distance from the top of the standpipe to the water level inside, is pushed up exactly one inch. The tube is again lowered into the shank as far as the marker and the pump is again started. The water level in the shank is soon drawn down to one inch below the original and thereafter holds steady, provided the suction is sufficient to remove the groundwater as fast as it can permeate through the gravel and enter the holes under the one-inch head. Water and air, then, are alternately being sucked into the flask. The rate of influx is measured by timing the rise of water in the flask between any two convenient marks. The temperature of the groundwater is noted. Then the permeability K in

centimeters per hour is read from the calibration curve (Fig. 5) for the observed temperature.

3. Second quantity measured is the dissolved oxygen concentration of the groundwater. A clean sample, about 20 ml., is pumped into a flask for measurement of its dissolved oxygen concentration O in grams per ml. by the abridged Winkler method (Harper, 1953) with a portable kit.

4. Last quantity measured is the hydraulic gradient. If the water in the standpipe is dirty, pumping should be continued under a low head until there is no visible murkiness in a sample tube full. Now about 5 ml. of roughly 1% methylene blue dye solution is pipetted (Fig. 6) into the standpipe. This dye is immediately mixed with the water inside the standpipe according to the stirring schedule and a sample is then withdrawn for an opacity measurement (Fig. 7) and the time noted. When the sample has been compared with the standards and its opacity decided upon and noted, it is quickly returned to the standpipe. Every 15 minutes the dye should be stirred three times according to the schedule. When it has been diluted 2 or 3 opacity numbers, a second sample is withdrawn for an opacity measurement immediately upon completion of a regular stirring. Again the time and opacity are noted. The rate of dye dilution is now computed, that is, the change in opacity number per hour $\frac{\partial n}{\partial t}$, and then the gradient S is read from the calibration curve (Fig. 19).

5. The apparent velocity V in centimeters per hour is computed from Darcy's Law, $V = KS$. Then the rate of oxygen supply in grams per square centimeter per hour to the redd is computed from the product VO .

Since a single value of either K or S is unreliable, several measurements of both should be made. It is suggested that three standpipes be driven (or one standpipe three times) two feet apart in a triangular pattern, that K and S be measured once in each standpipe and that the three products KS be averaged. The oxygen concentration need be measured once only.

ACKNOWLEDGMENTS

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The Relation between Scale Diameter and Body Length of Kamloops Trout, *Salmo gairdneri kamloops*¹

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ABSTRACT

The scale/body relationship for Kamloops trout is very close to direct proportion for fish larger than 4.5 cm. fork length. The resultant plot on a double logarithmic grid is linear with a slope not significantly different from 1.00 (45°). Calculations of lengths of trout from scales at ages previous to that of capture can be made on the basis of simple proportion in two ways, (1) by use of a constant slope (45°) on a double logarithmic plot, or (2) by use of a constant zero-zero intercept on an arithmetic plot.

Growth of the scales of the young is characterized by relatively rapid increase from time of scale formation, 3.5 cm. fork length up to 4.5 cm. At about 4.5 cm. fork length there is a sharp break (inflection) in the relative growth curve toward isometric growth of scales and body. Reliable estimates of the length of trout may be obtained from scales alone, using the diameter of the first circulus of the scale, the slopes and inflection of the relative scale/body plot and total diameter of the scale at time of capture.

Marked Kamloops trout of known size were released in 1953. Subsequent recaptures both in 1953 and 1954 substantiated the accuracy of the method of estimating lengths of trout at ages previous to that of capture.

Observations on the steelhead trout, *Salmo gairdneri gairdneri*, and on the coastal cut-throat trout, *Salmo clarki clarki*, suggest that an isometric scale/body relationship may exist among those species also.

INTRODUCTION

RATE of growth and age composition are two fundamental aspects of the vital statistics of fish populations. The scales of many species of fish lend themselves to ready interpretation of annual periods of growth, while knowledge of the mathematical relation between scale size and body size makes possible the computation of fish lengths at ages previous to that of capture. Although considerable variation may be observed in the methods employed in estimating fish lengths from scales, most workers have followed the general formula outlined by Fraser (1920). Briefly, in Fraser's method a linear relationship is assumed between scale growth and body growth but often it is necessary to correct direct-proportion calculated lengths if the scale/body ratio is not constant over all ranges in lengths of fish. Slightly different applications of Fraser's method may be found in Ricker (1942), Van Oosten (1942) and Fry (1943).

This study attempts no comparison between the scale/body relation of Kamloops trout and the relation observed for other species. Brief mention, however, will be made in a following section to other work in progress at this laboratory,

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dealing with the scale/body relationships of the coastal cutthroat trout, *Salmo clarki clarki*, and the steelhead trout, *Salmo gairdneri gairdneri*.

The present study was carried out as a portion of the research program of the Fisheries Management Division of the British Columbia Game Department and through the Department of Zoology at the University of British Columbia.

MATERIALS AND METHODS

Scale measurements of Kamloops trout from Paul Lake, British Columbia, provided the data on which was based the study of the relationship between scale diameter and body length of over-yearling fish. Observations on the length of trout at the time scales are first formed, and the relation between scale diameter and fork length of young trout, were made on two groups of 248 and 40 specimens, respectively. These fish were obtained from Pinantan Lake stock, reared at the B.C. Game Department trout hatchery at Smith's Falls, Cultus Lake, B.C. Equal numbers of trout from Beaver Lake hatchery, near Kelowna, B.C. were reared to yearling age in a natural rearing pond at Kelowna and at the B.C. Game Department trout hatchery at Summerland, B.C. These fish were released in Corbett Lake, near Merritt, B.C. Subsequent recapture of 72 individuals in Corbett Lake in November, 1953, and 34 specimens of the same stock from June through September, 1954, provided data for a check on the method of computation of fish lengths from scales.

RELATION BETWEEN SCALE DIAMETER AND BODY LENGTH

OVER-YEARLING TROUT. Measurements of scale diameters were made for 1,322 Kamloops trout sampled from the sport fishery at Paul Lake, B.C., over the period 1946 to 1952. These measurements (dorso-ventral diameters) were grouped according to each centimeter of fork length throughout the total range in the samples. The data were then transformed to logarithms and the regression of scale diameter on fork length was calculated for the range 16.5 cm. to 45.0 cm. (Fig. 1). The resultant value ($b = 0.985 \pm 0.064$) did not differ significantly from the value ($b = 1.01$) which may be derived from the data presented by Mottley (1942) for Kamloops trout from Paul Lake. In addition, neither of the two values differs significantly from a regression slope of 1.00. The discrepancies between the data presented by Mottley and the present study probably arose through sampling error and not through any real change in length/scale relationship.

It is apparent that the scales of Kamloops trout in Paul Lake grow very nearly in direct proportion to growth in body length. Furthermore, a straight line on a logarithmic plot with a slope of 1.00 (45°) has an intercept of zero-zero on an arithmetic plot. For means of back-calculation then, no correction is needed, provided that the relationship between scale diameter and body length is constant over the range through which the calculations are to be made.

YOUNG TROUT. Scales from 40 small Kamloops trout of Pinantan Lake stock which ranged in length from 3.70 cm. to 9.61 cm. were measured under an

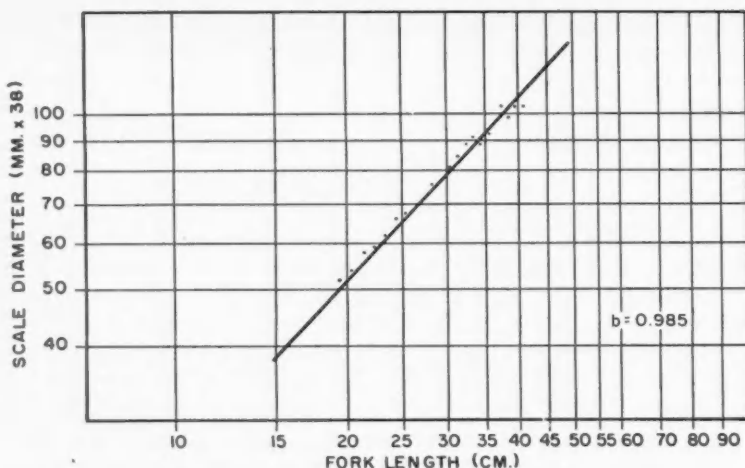


FIGURE 1. Scale/body relationship of over-yearling Kamloops trout.

ocular micrometer. The logarithm of mean diameter of 10 scales from each specimen was plotted (y axis) against the logarithm of fork length (x axis) for that specimen. The resultant plot indicated a sharp inflection toward decreased growth of the scales relative to fork length at the point which corresponded to approximately 10 mm. scale diameter (X 38) and fork length approximately 4.5 cm. The sample of trout was then subdivided into two portions: (1) fish

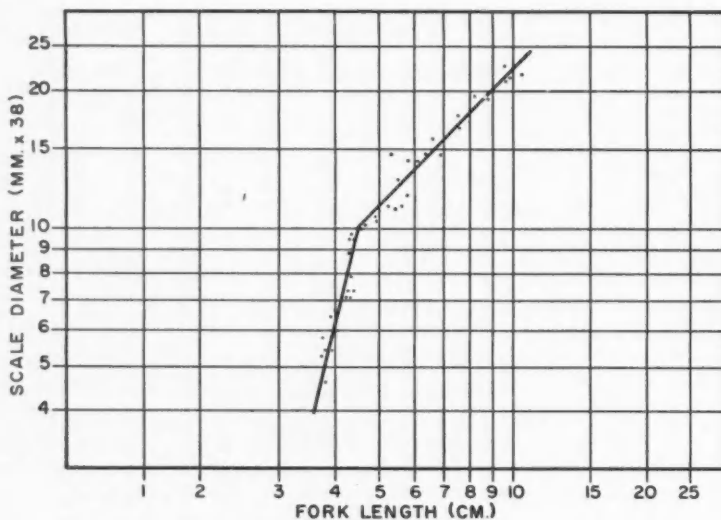


FIGURE 2. Scale/body relationship of young Kamloops trout.

with a fork length in excess of 4.5 cm. and (2) fish with a fork length less than 4.5 cm. Slope of the scale/body plot below fork length 4.5 cm. was found to be 3.99 while the slope of the scale/body plot for fish in excess of 4.5 cm. was found to be 1.024. A significant statistical difference could not be demonstrated between the slope of 1.024, the values outlined previously for the Paul Lake trout, or a slope of 1.00. The data are presented in Figure 2.

It may be argued that the fitting of two straight lines to the data is arbitrary, and that three or more straight lines or a curve might better describe the scale/body relation at or near the point of inflection. The practical advantages and theoretical significance of fitting two straight lines to growth data of this type are adequately discussed and recommended by Martin (1949).

LENGTH OF TROUT AT TIME OF SCALE FORMATION. A regular, weekly series of young trout, from hatching (2.5 cm.) to approximately 5 cm. fork length was obtained from Smith's Falls trout hatchery at Cultus Lake, B.C. Scales were first observed to have formed in a sample of trout with a mean fork length of 3.56 cm. All the fish in this sample (248) were then examined to determine on which specimens scales were present. The skin of each fish was scraped with a fine scalpel in the mid-region, between the lateral line and the dorsal fin. The mucous substance which adhered to the scalpel blade was examined under a microscope at 100 magnifications. Length of each specimen was obtained to the nearest 0.1 mm. by means of a vernier caliper, to the jaws of which had been affixed fine needles.

Table I lists the length and presence or absence of scales for 38 Kamloops trout of the total sample of 248. No scales were present on any fish of less than 3.38 cm. fork length, nor were scales absent from any fish in excess of 3.71 cm. fork length. If 3.38 cm. is assumed to be the smallest length at which fish form scales and 3.71 cm. to be the greatest length at which scales have not formed, then the mid-point of this range (3.54 cm.) would indicate the average length at which scales form on this part of the body.

TABLE I. Sample of young Kamloops trout arranged in order of fork length (in cm.) with those which bore scales indicated by an asterisk.

2.87	3.39	3.55*	3.88*
2.93	3.45	3.56*	3.89*
2.95	3.46*	3.57	3.90*
2.96	3.47	3.59*	3.90*
3.00	3.47	3.64	3.90*
3.18	3.48	3.69	4.03*
3.21	3.48	3.71*	4.10*
3.23	3.51*	3.72*	4.26*
3.29	3.54	3.78*	4.29*
3.38*		3.83*	

CALCULATIONS OF LENGTHS FROM SCALE DIAMETERS

LENGTHS OF FISH AT AGES PREVIOUS TO CAPTURE

Any method of estimating lengths of fish at ages previous to that of capture should (1) be simple in operation, to facilitate the handling of large masses of

data and (2) give sufficient accuracy of estimation that back-calculation may be handled by appropriate statistical tests. It is indicated that the method outlined below fulfils both requirements.

If the relationship between scale diameter and body length is proportional, i.e. if a fish is to have relatively the same coverage of scales at all lengths, the slope of a line measuring this relationship will be 45° on a logarithmic plot. Since the slope of the plot of scale diameter on body length for Kamloops trout did not suffer significantly from 45° , that value was used in all calculations. Simply the method is as follows:

A straight-edge was fitted near the lower border of a sheet of double logarithmic graph paper and a plastic 45° square was laid over the paper. Parallel to the hypotenuse a fine line was scratched on the surface of the square which would be in contact with the paper. With the base of the square in contact with the straight-edge, the square could be slid easily in a direction at right angles to the "Y" axis of the graph paper (Fig. 3).

In order to estimate fish length from scale diameter, the 45° square was moved so that the fine hairline on its under surface coincided with the point which indicated scale diameter and fork length of fish at time of capture. To obtain length of fish at earlier ages, the hairline was followed down until it

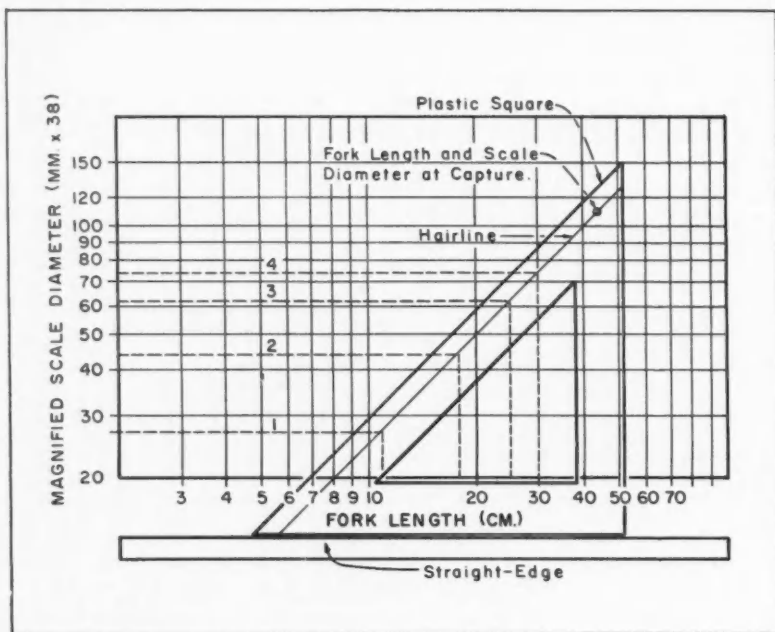


FIGURE 3. Calculation of length of fish at ages previous to that of capture. Dotted lines indicate the scale diameter and respective fork length at each annular growth check from ages 1 to 4.

intersected the line giving the value on the "Y" axis which corresponded to the magnified diameter of the scale at the desired annular "growth check." Fork length was then read off directly below on the "X" axis. With the appropriate size of grid, lengths may be estimated to the nearest 0.1 cm.

The above method is one of simple proportion. Its chief advantage lies in the fact that no calculations are necessary when making estimates of length, thus large masses of data may be handled with rapidity.

Calculations assuming direct proportion between scale diameter and body length may also be made on an arithmetic plot, using a zero-zero intercept and variable slope for each estimate. In the present study the double logarithmic plot and set square were used because they obviated the necessity for construction of an accurate movable arm fixed at its zero-zero end.

ESTIMATES OF LENGTHS FROM SCALES ALONE

The scale/body relation of Kamloops trout is characterized by rapid growth of the scale relative to body growth during early development and by a sharp inflection of the relative growth curve at fork length approximately 4.5 cm., after which the scale/body relation is directly proportional (Figs. 1, 2). Although observations on the growth of individual scales do not appear in the literature, it is apparent from scale markings of Kamloops trout that most scales on any specimen follow a similar pattern. On each scale may be observed concentric rings, and on most may be observed similar periods of accelerated or retarded growth, depending chiefly upon the environment to which the fish has been subjected.

It is likely also, then, that scales of Kamloops trout provide estimates of lengths of the individuals on which they grow, from the time scales first appear in their pockets or placodes in the skin as definitive structures. If the foregoing is correct, any scale which arises in a relatively large pocket will remain relatively large, and any scale which arises in a relatively small pocket will remain relatively small.

Figure 4 illustrates the way in which initial size of the scale (diameter of first circulus) and total diameter of the scale at time of capture may be combined to provide an empirical estimate of length for Kamloops trout. In Figure 4 the observed range in first circulus diameter for the sample in question is marked out at 0.5-mm. intervals along the dotted line "S" which corresponds to 3.5 cm. fork length, the average length at which Kamloops trout form scales. With logarithmic slope 3.99 (from Fig. 2), parallel lines are drawn from the 0.5-mm. intervals on the solid base line "S" to intersect the dotted line "I". This line corresponds to 4.5 cm. fork length, the average length where inflection occurs in the relative growth curve for scales of Kamloops trout. From the points of intersection on the dotted line "I" the lines are projected on a slope of 1.00 (45°). These projected lines represent the proportional increase in scale and body size beyond fork length 4.5 cm.

In order to estimate the length of a fish from its scales, first-circulus diameter and total scale diameter are measured. Using first-circulus diameter as a datum

TABLE II. Measured fork lengths and fork lengths estimated from first circulus diameters and total scale diameters of the scales of 31 Kamloops trout from Paul Lake, B.C.

First circulus diameter ($\times 38$)	Total scale diameter ($\times 38$)	Estimated fork length	Actual fork length	Error in estimate
<i>mm.</i>	<i>mm.</i>	<i>cm.</i>	<i>cm.</i>	<i>cm.</i>
4.0	83	35.0	34.0	+1.0
5.5	90	28.5	28.5	0.0
5.0	91	31.5	29.5	+2.0
5.5	92	29.5	30.5	-1.0
4.5	77	29.5	29.5	0.0
5.0	72	25.0	24.0	+1.0
5.0	79	27.0	23.5	+3.5
5.5	88	28.0	29.0	-1.0
4.5	91	34.5	33.5	+1.0
4.5	91	34.5	35.0	-0.5
5.0	74	25.5	26.0	-0.5
5.0	79	27.5	25.5	+2.0
4.0	55	23.0	22.5	+0.5
4.5	69	26.0	25.5	+0.5
5.5	89	28.5	29.5	-1.0
5.0	88	30.5	29.0	+1.5
4.5	81	30.5	29.0	+1.5
4.0	76	31.5	27.5	+4.0
5.0	82	28.5	31.0	-2.5
6.0	87	25.5	30.0	-4.5
4.5	69	26.5	28.5	-2.0
5.0	82	28.5	27.0	+1.5
6.0	65	19.0	22.0	-3.0
4.5	63	24.0	25.0	-1.0
4.5	64	24.5	22.5	+2.0
5.5	62	20.0	26.0	-6.0
4.5	64	24.5	24.0	+0.5
4.0	54	22.5	22.0	+0.5
3.5	46	21.5	22.5	-1.0
4.5	57	22.5	22.5	0.0
5.0	81	28.0	33.0	-5.0
Means		27.15 \pm 0.73	27.34 \pm 0.68	1.68
		σ = 4.06	σ = 3.79	

point on the base line "S", the appropriate line is followed on the plot until it intersects the line which corresponds to total scale diameter on the "Y" axis of the grid. Fork length is then read off directly below on the "X" axis.

Table II summarizes the results of a series of 31 predictions of fish lengths, using the method described above. There was no significant difference between the means of estimated and actual lengths ($P < 0.01$), nor was there a significant difference between the variances. However, a maximum error of 6.0 cm. occurred in one estimate, and average error was 1.68 cm. (6.1%). There was no correlation between the direction of error and the size of fish. Correlation value between the predicted and actual lengths was 0.85 ($P < 0.001$).

It should be pointed out that the method illustrated above is of an empirical nature. In addition, errors in estimate of considerable magnitude can be expected. However, the method may provide the means of studying early growth histories of spawning trout or salmon, the scales of which become heavily eroded, thus rendering the scale border useless as a reference point for calculations of lengths.

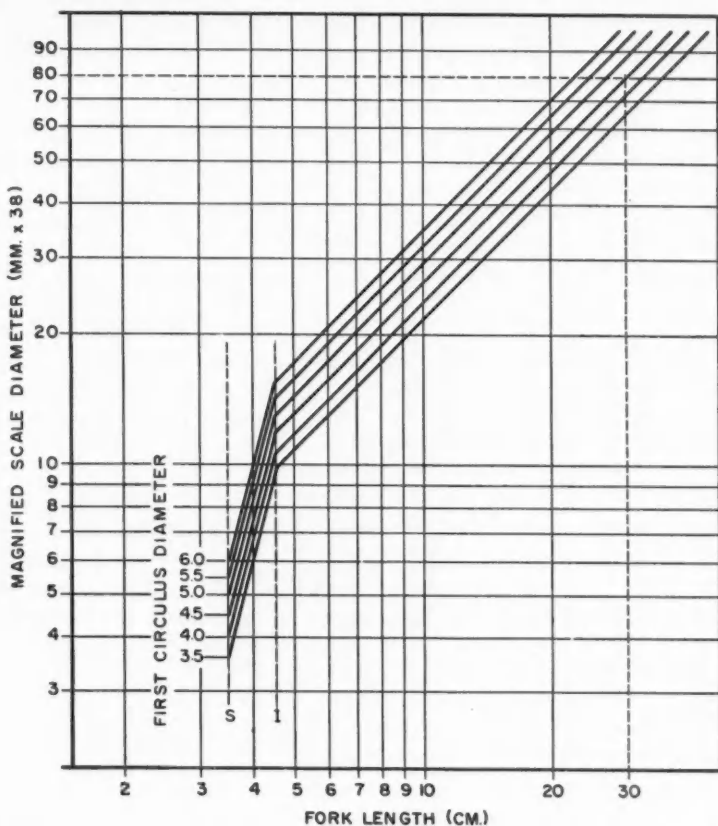


FIGURE 4. Use of scales of Kamloops trout to estimate lengths without reference to length at capture.

A CHECK ON THE METHOD OF ESTIMATING FISH LENGTHS FROM SCALES

During the course of experimental lake stocking in 1953 it was found possible to use two groups of trout to obtain a check on the reliability of the method for estimating lengths of trout at ages previous to that of capture. Equal numbers of trout from Beaver Lake Hatchery, near Kelowna, B.C., were reared at Summerland Hatchery and in natural outdoor ponds at Kelowna. Both groups were marked by fin-clipping and released in Corbett Lake, near Merritt, B.C. Group A (reared at Summerland) averaged 10.5 cm. at release, while Group B (reared at Kelowna) averaged 7.02 cm. at release. During October and November, 1953, a total of 32 Group A and 40 Group B trout were recaptured by gillnetting and angling. In 1954 angling and gillnetting resulted in recapture

of 23 Group A and 11 Group B trout. Table III summarizes actual mean fork lengths at release in 1953 and at recapture in 1953 and 1954 for both groups of trout, and estimated mean fork lengths at release for the two groups of trout made separately from scales of 1953 and 1954 recaptures.

Table III shows that mean length at release as estimated from scales of recaptures agrees closely with actual mean length at release for both groups of trout. Although the estimated and actual lengths at release did not differ significantly, the estimated lengths for both groups were slightly smaller from 1954 recaptures than for 1953 recaptures. In the case of Group A, estimates in both 1953 and 1954 were below the actual mean length at release, and for Group B were slightly above.

Comparing estimates of the mean length of each group from 1953 to 1954 might be suggestive of "Lee's phenomenon". Earlier studies (Ricker, 1942; Larkin and Smith, 1953) indicate that "Lee's phenomenon" may be introduced artificially by selective fishing methods. It may also be present as a real factor in the scale/body relationship, although not of very great importance in this case. Comparison of the estimates of mean length between each group within each year was suggestive of variation which would be expected in biological data of this nature. In any event, the empirical scale/body slope of 45° (which agrees very closely with the scale/body relation of Paul Lake trout) appeared to be adequate to estimate the length of trout from another population (Beaver Lake trout) over a range of growth of more than 20 centimeters for each group.

TABLE III. Mean fork length at release and at recapture and mean length at release estimated from scales of recaptured trout in Corbett Lake, B.C., 1953 and 1954. All lengths in centimeters.

Group	Fork length at release	Fork length at capture		Estimated length at release	
		1953	1954	1953	1954
A	10.5	23.7	33.8	10.1	10.0
B	7.02	19.4	28.9	7.23	7.03

SCALE/BODY RELATIONSHIP IN OTHER SALMONIDS

Since the scale/body relationship was worked out for Kamloops trout, similar data have become available for the steelhead trout, *Salmo gairdneri gairdneri*, and the coastal cutthroat trout, *Salmo clarki clarki*. McMynn and Vernon (personal communication) have shown the relationship in cutthroat trout to be linear with a log-log regression line slope of 1.019. Maher and Larkin (1955, in press) also found the relationship for steelhead trout to be linear on a double logarithmic plot with a slope of 1.010. The plots for these three species of *Salmo* are shown in Figure 5.

None of the three lines differs significantly from a slope of 1.00, indicating that the relative growth of scales and body is very close to direct proportion for all three groups. The use of an empirical slope of 45° on a double logarithmic

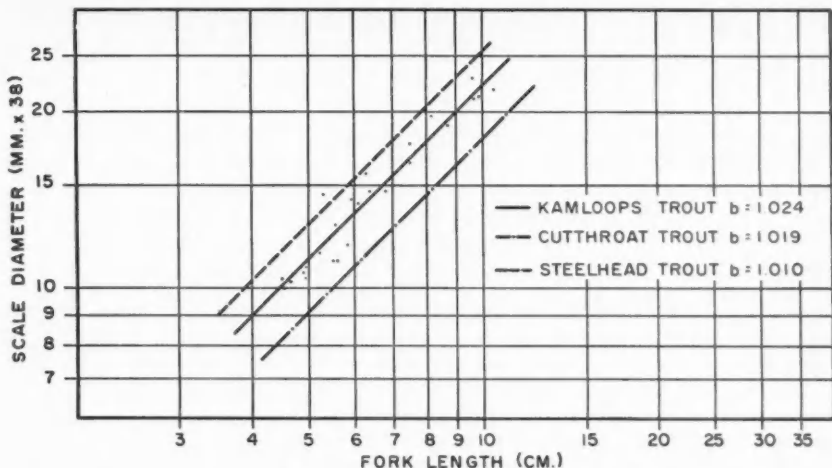


FIGURE 5. Scale/body relationships of young Kamloops, cutthroat and steelhead trout.

plot probably is accurate enough for practical purposes of calculating lengths from scales in these groups of *Salmo*.

It may be observed that the three regression lines in Figure 5 are rather widely dispersed on the vertical axis. This may be explained by the difference in scale size. The appropriate statistical test (Snedecor, 1950, p. 120) shows that the mean value of \bar{Y} (scale diameter) at any fork length for steelhead is significantly greater than for Kamloops trout, while the corresponding value for Kamloops trout is significantly greater than that for cutthroat trout. In each case $P < .01$.

DISCUSSION

The use of the scales of fishes to estimate lengths at ages previous to that of capture is a valuable technique in fisheries biology. Examination of the scale/body relationship for different species has revealed many variations. Van Oosten (1942), Hile (1941) and Ricker (1942) described differences of considerable magnitude in the scale/body relation for some Centrarchidae. Each of these authors suggests the need for further investigation of some of the possible factors involved, such as seasonal variation in the scale/body relation, variation caused by differences in growth rates, hereditary differences and so forth. Van Oosten stressed that it would be dangerous to use for one species a general formula developed for even another population of that species, especially if the samples were from different areas.

Examination of the literature on this subject would suggest that all data should first be plotted graphically. If the relationship appears to be linear, analysis of regression should be used as the basis for reducing the data to a formula which can be applied either to arithmetic calculations or to operation

of nomographic devices. Care should be exercised so that any formula which is to be used for purposes of calculations of lengths will not be affected by variability in scale size at any one length on either side of the line of best fit.

In this regard, Dr. Ralph Hile (personal communication) describes a formula which resulted in errors of estimates made from scales of different sizes. The body/scale relationship was observed to be:

$$\begin{aligned} \log L &= \log c + b \log S & (1) \\ \text{when } L &= \text{length of fish} \\ S &= \text{scale size} \\ b \text{ and } c &= \text{constants.} \end{aligned}$$

From the above equation may be derived the following formula:

$$\begin{aligned} \log L_n &= \log c + \log S_n \frac{\log L_T - \log c}{\log S_T} & (2) \\ \text{when } n &= \text{year} \\ T &= \text{time of capture.} \end{aligned}$$

This formula can give accurate results only when the scale measured happens to be of *exactly* theoretical size as prescribed by (1). If the scale deviates from theoretical size, estimates of lengths are in error. The formula would have been usable had $\log c$ been eliminated, rather than b , to obtain:

$$\log L_n = \log L_T + n (\log S_n - \log S_T) \quad (3)$$

With this formula, estimates of L_n are independent of actual scale size since the values of $(\log S_n - \log S_T)$ depend only on the ratio S_n/S_T .

Essentially, use of a double logarithmic grid, where back-calculations are made along the same slope for each specimen, results in elimination of the constant c , described above. In the case of the three kinds of *Salmo*, the scale/body relationship is a special one. Returning to (3) and substituting the assumed value $n = 1$, the following is obtained:

$$\log L_n = \log L_T + \log S_n - \log S_T$$

which reduces to $L_n = L_T \frac{S_n}{S_T}$. The last equation clearly is nothing more than the direct proportion formula. From another approach, the equation: $\log L = \log c + n \log S$ or $L = c S^n$. Where $n = 1$, then $L = c S$, which is a straight line passing through the origin.

There is little chance of ever observing exactly a proportionate scale/body relationship in any population of fish. In addition, it would appear from published accounts for many species, including the three groups of *Salmo* described herein, that generally the scale/body ratio increases with age (size). However, in the present examples, where the observed relationship is very close to proportional, whatever error occurs will be small and consistent from using the very convenient slope of 45° along which calculations are made. If the slope of the plot is less than 45° , as was the case with older Paul Lake trout, estimates of lengths at ages previous to that of capture will be slightly too large. The con-

verse will be true if the observed slope is greater than 45° on a double logarithmic plot. Where the limits of the observed regression slope clearly overlap a value of 1.00, the convenience of using a slope of 1.00 would appear to outweigh the small errors which result.

Mottley (1942) showed that scale diameters of Kamloops trout of Paul Lake could be compared directly to provide unbiased estimates of growth. This is particularly true where the growth of trout is rapid and lengths of the various age classes do not overlap. An attempt was made to apply Mottley's suggested method to comparisons of growth rate of trout in Paul Lake in later years. However, by 1949 growth of the various age groups had become so variable that no efficient comparisons could be made by using scale diameters only as estimates of lengths. In some cases, differences of as much as 100 per cent occurred in total scale diameters at capture of fish of the same age group. Individual growth histories were therefore calculated (Larkin and Smith, 1954) using the method outlined in this presentation.

As mentioned previously, a sharp inflection occurs in the relative growth curve for scales and body length of Kamloops trout. Lengths previous to capture therefore cannot be safely estimated at or near the scale size (about 10/38 mm.) where inflection occurs. Little difficulty however is experienced with most Kamloops trout since most specimens have attained a scale size well above the inflection point (generally about 15/38–20/38 mm.) by the time the first annulus has formed.

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**A Comparison of Atlantic Sea Sturgeon with a New
Subspecies from the Gulf of Mexico
(*Acipenser oxyrhynchus de sotoi*)^{1, 2}**

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ABSTRACT

The sea sturgeon, *Acipenser oxyrhynchus* Mitchill, occurs in the western north Atlantic Ocean from Canadian waters south to the Gulf of Mexico. Specimens taken from eastern Florida to Quebec are assigned to the typical subspecies *oxyrhynchus*, while 2 specimens from off Mississippi are here described as the new subspecies *de sotoi*. The latter differs in having a longer head, longer pectoral fins, strongly developed scutes of distinctive shape and an unusually long spleen.

THANKS to Dr. Loren P. Woods, Curator of Fishes, Chicago Natural History Museum, we received for identification 3 sturgeon from the southern United States. One of them (No. 35376) was collected by T. Surber, at New Berlin (near Jacksonville), Florida, January 6, 1900. Two others (Nos. 59803 and 59804) were obtained by T. Dawson, between Twin and Rabbit Islands, at the mouth of Singing River, off Gautier, Mississippi, on November 30, 1953. All these fish were young, immature, ranging in fork length from 50 to 60 cm.

Upon examining these specimens and comparing them with those from Quebec and New York, we identified them as *Acipenser oxyrhynchus* Mitchill 1814, by the following characteristics: a fontanelle between the frontal and parietal plates (in the smaller specimen); all scutes well-developed, and those of dorsal and lateral rows pale in colour, contrasting with dark background of surrounding parts of the body; mouth small; head long; low number of gill-rakers; and white unpigmented viscera.

While the Florida specimen agrees closely with Quebec sturgeon, the two Gulf of Mexico fish are definitely different. We propose, therefore, to separate them into a distinct, southern subspecies, *Acipenser oxyrhynchus de sotoi*,³ subsp. nov. Although sea sturgeon from different rivers along the eastern Atlantic coast have never been studied in detail, at least superficially they resemble the typical population of New York, from which locality come the type of *A.*

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³The name was suggested by Dr. L. P. Woods, in honor of Fernando de Soto, the sixteenth-century Spanish captain who explored the Gulf of Mexico region. For further details on de Soto, consult Galtsoff (1954, p. 14) and particularly United States de Soto Expedition Commission (1939).

oxyrhynchus. Therefore the specimens from eastern Florida to Quebec could be considered tentatively as belonging to a northern, typical subspecies, namely, *A. oxyrhynchus oxyrhynchus* Mitchill.

The two subspecies are easily distinguishable by body proportions, differences in the shape and degree of development of the scutes, as well as in details of interior anatomy.

Acipenser oxyrhynchus de sotoi, subsp. nov.

DIAGNOSIS

The subspecies *de sotoi* is distinguishable from typical *oxyrhynchus* of comparable sizes by a longer head (30.9–33.6% of FL.) and longer pectoral fins (15.6–16.3% of FL.). The other details are given in Tables I–III. All scutes in *de sotoi* are very strongly developed, and of characteristic shape: the length is much shorter than the width. Moreover, the spleen in *de sotoi* is unusually long, extending from the pyloric apparatus⁴ to the lower end of the loop of the small intestine (Plate VII), or nearly so, while in subspecies *oxyrhynchus* this gland does not reach below the middle of this loop.

TABLE I. Measurements in millimeters of sea sturgeon of the two different subspecies.

Subspecies	<i>A. oxyrhynchus de sotoi</i>		<i>A. oxyrhynchus oxyrhynchus</i>					
	Gulf of Mexico		Florida	Quebec				
Catalogue Nos.	59803	59804	35376	425	442	876	508	877
Total length (TL)	580?	655	547	545	578	655	690	715
Fork length (FL)	515	595	483	485	515	580	595	620
Head length (T)	173	184	132	134	137	160	159	164
Diameter of eye (O)	12.5	12.5	10	10	10	11.5	10	12
Interorbital space (i)	38	49	36	36	38	43	43	47
Length of snout (ML)	98	97	73	74	74	84	80	86
Post orbital distance (pO)	63	74	52	64	70	77	80	83
Maximum body depth (H)	81	93	75	62	71	73	96	88
Minimum body depth (h)	18	21	17	16	17	21	20	20
Length of caudal peduncle (pc)	85	104	85	85	92	98	110	114
Width of mouth (Be)	30	39	25	26	28	36	37	34
Length of pectoral (P)	80	97	62	64	64	80	82	86
Length of ventral (V)	44	49	32	39	39	44	47	44
Distance between P and V (P-V)	174	205	186	185	202	217	221	229
Distance between V and anal (V-A)	66	81	65	64	70	77	80	83

⁴The "pyloric apparatus", according to a term used by Ryder (1890, p. 246), is a compact organ, made of numerous pyloric caeca, surrounded by a solid tunic of connective tissue. This compound racemose gland opens into the duodenum, immediately below the stomach, which in *A. oxyrhynchus* is not very extended nor very muscular.

TABLE II. Body proportions of sea sturgeon, expressed in percentages.

Subspecies	<i>A. oxyrhynchus de sotoi</i>			<i>A. oxyrhynchus oxyrhynchus</i>						
	Gulf of Mexico			Florida	Quebec					
Locality Body proportions	59803	59804	Mean	35376	Mean	425	442	876	508	877
FL (mm.)	515	595	555	483	559	485	516	580	595	620
T/FL	33.6	30.9	32.3	27.3	27.0	27.6	26.6	27.6	26.7	26.5
ML/FL	19.0	16.3	17.7	15.1	13.7	15.3	14.4	11.6	13.4	13.9
pO/FL	12.2	12.4	12.3	10.8	10.6	9.0	10.3	11.6	10.8	11.1
H/FL	15.7	15.6	15.7	15.5	13.9	12.8	13.8	12.6	16.1	14.2
pc/FL	16.5	17.5	17.0	17.6	17.8	17.5	17.9	16.9	18.5	18.4
P/FL	15.5	16.3	15.9	12.8	13.4	13.2	12.4	13.8	13.8	13.9
V/FL	8.5	8.2	8.4	6.6	7.6	8.0	7.6	7.6	7.9	7.1
Be/T	17.3	21.2	19.3	18.9	21.3	19.4	20.4	22.5	23.3	20.7
O/T	7.2	6.8	7.0	7.6	7.1	7.5	7.3	7.2	6.3	7.3
i/T	22.0	26.6	24.3	27.3	27.9	26.9	27.7	26.9	29.6	28.7
Be/i	78.9	79.5	79.2	69.4	77.6	72.2	73.7	83.7	86.0	72.3
P/P-V	46.0	47.3	46.7	33.3	35.6	34.6	31.7	36.9	37.1	37.6
V/V-A	66.7	60.5	63.6	49.2	57.1	60.9	55.7	57.1	58.8	53.0
h/pc	21.2	20.2	20.7	20.0	18.9	18.8	18.5	21.4	18.2	17.5

TABLE III. Averages in millimeters of principal body parts of two subspecies of *A. oxyrhynchus*.

Subspecies	<i>de sotoi</i>	<i>oxyrhynchus</i>
Locality	Gulf of Mexico	Florida and Quebec
Number of specimens	2	6
FL	550.0	546.3
T	178.5	147.7
O	12.5	10.6
i	43.5	41.2
ML	97.5	78.5
MV	103.0	81.0
pO	68.5	59.0
pc	17.0	17.8
H	87.0	77.5
h	19.5	18.5
P	88.5	73.0
V	46.5	40.8
P-V	189.5	206.7
V-A	73.5	73.2

TYPE

As a holotype, we selected a smaller specimen, carrying the Chicago Museum No. 59803, which will be deposited in the collections of the U.S. National Museum, Washington, D.C. Its fork length is 515 mm., the total length is about 580 mm., but could not be given accurately as the extremity of the upper caudal lobe is broken. The larger specimen (No. 59804), with respective lengths of 595 mm. and 655 mm., is paratype and will remain in the collections of the Chicago Natural History Museum.

The holotype possesses the following characters, counted on left side of the fish: 11 dorsal scutes, 26 lateral scutes, 10 ventral scutes, and 20 gill-rakers.



PLATE I. Dorsal view of the holotype (No. 59803) of *A. oxyrhynchus de sotoi*.



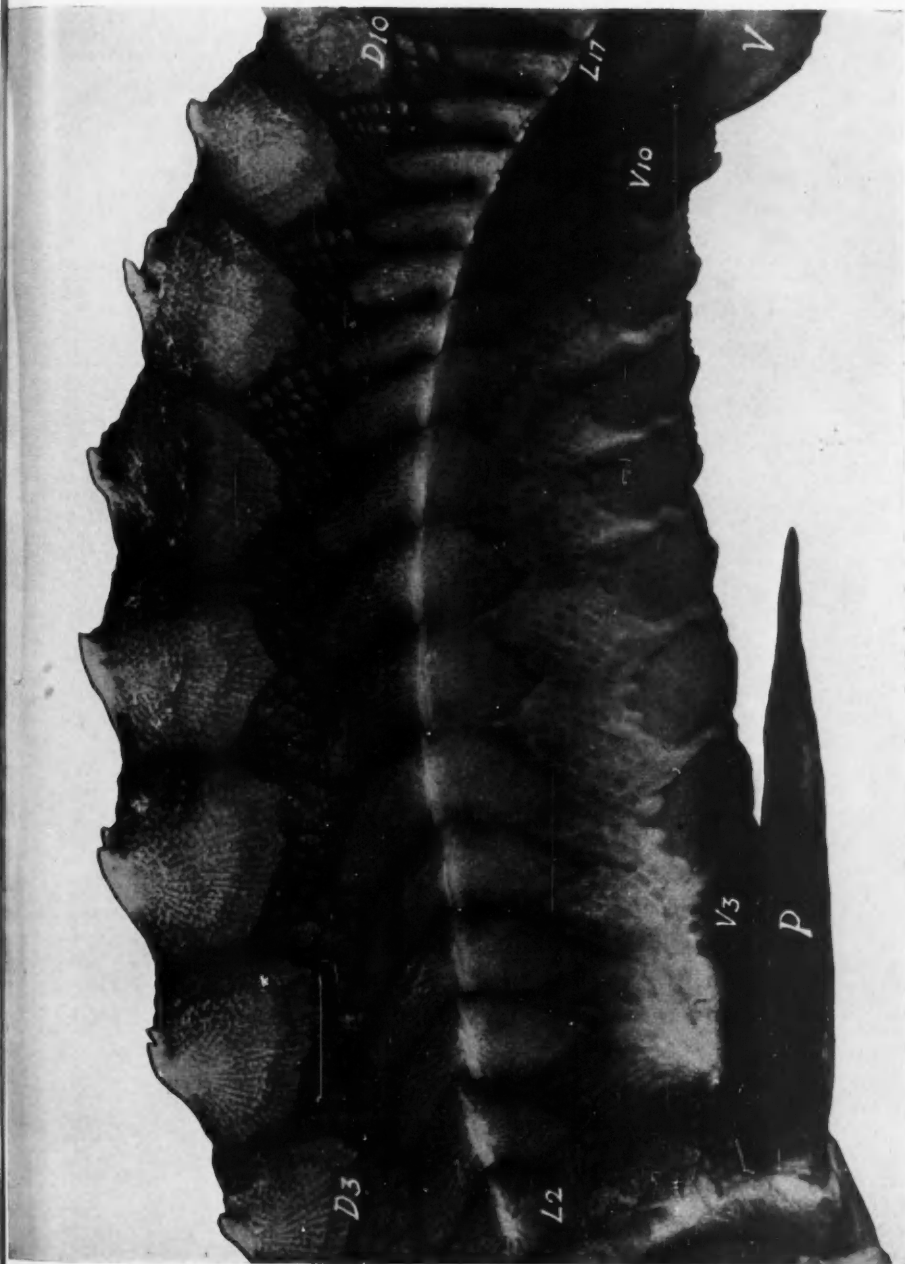


PLATE III. Close-up of the side of the holotype of *A. oxyrinchus de sotoi*: D3 and D10-3rd and 10th dorsal scutes; L2 and L17-2nd and 17th lateral scutes; P-pectoral fin; V-ventral fin; V3 and V10-3rd and 10th ventral scutes.

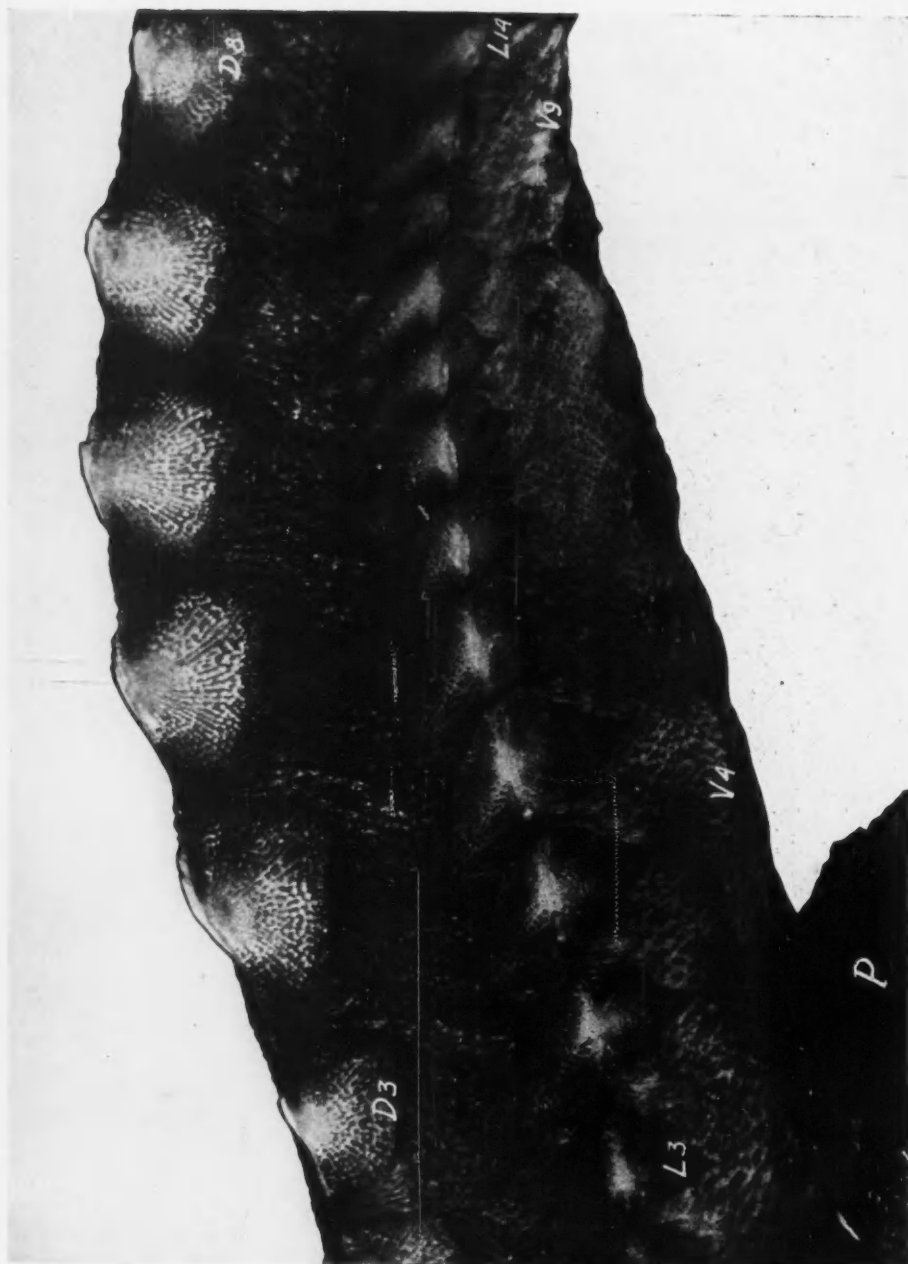


PLATE IV. Side view of *A. oxyrhynchus oxyrhynchus* (No. 876) from Quebec. For explanation see Plate III.

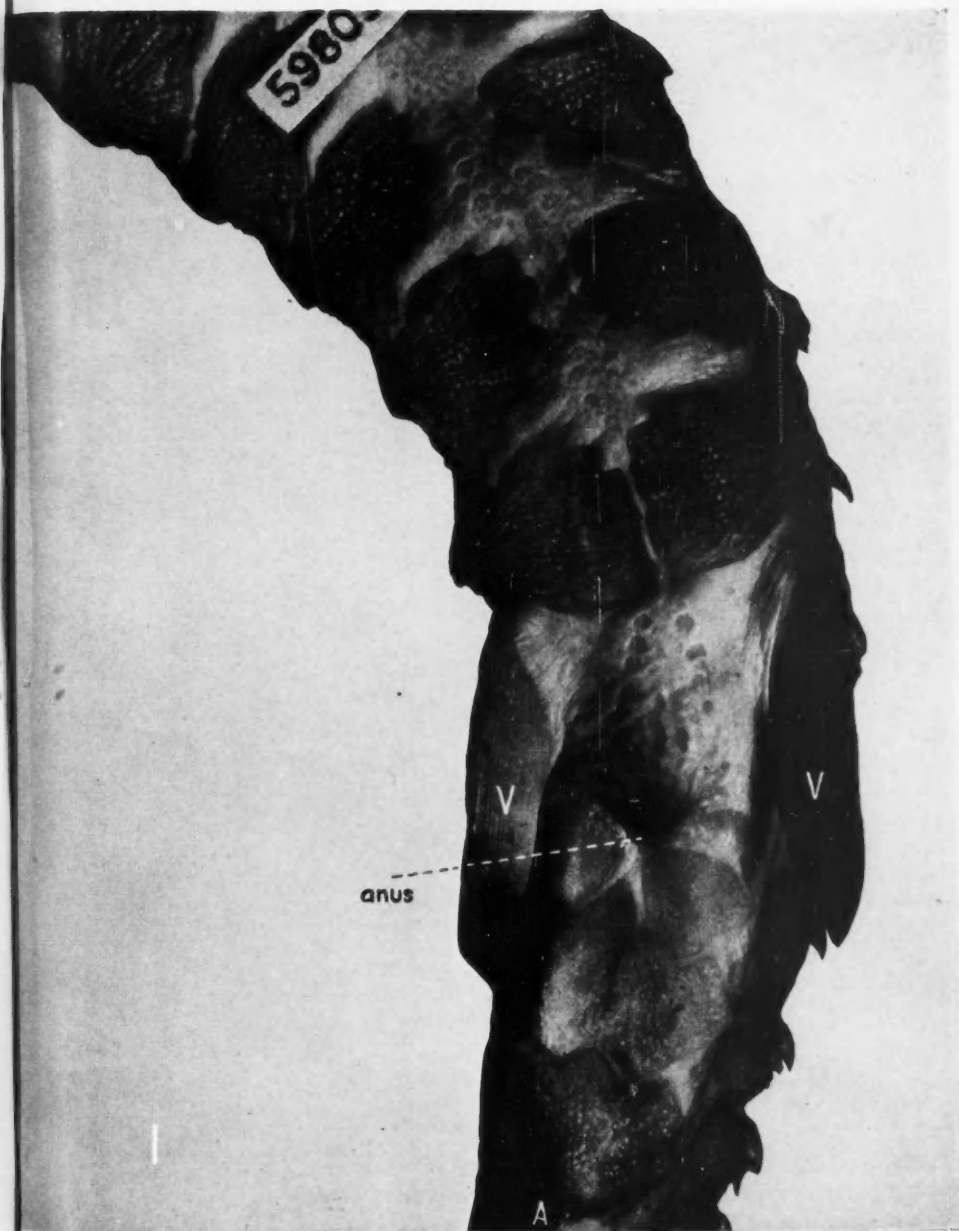


PLATE V. Ventral scutes of the holotype of *A. oxyrhynchus de sotoi*: A—anal fin; V—ventral fins.



PLATE VI. Ventral scutes of *A. oxyrhynchus oxyrhynchus* (No. 876) from Quebec.

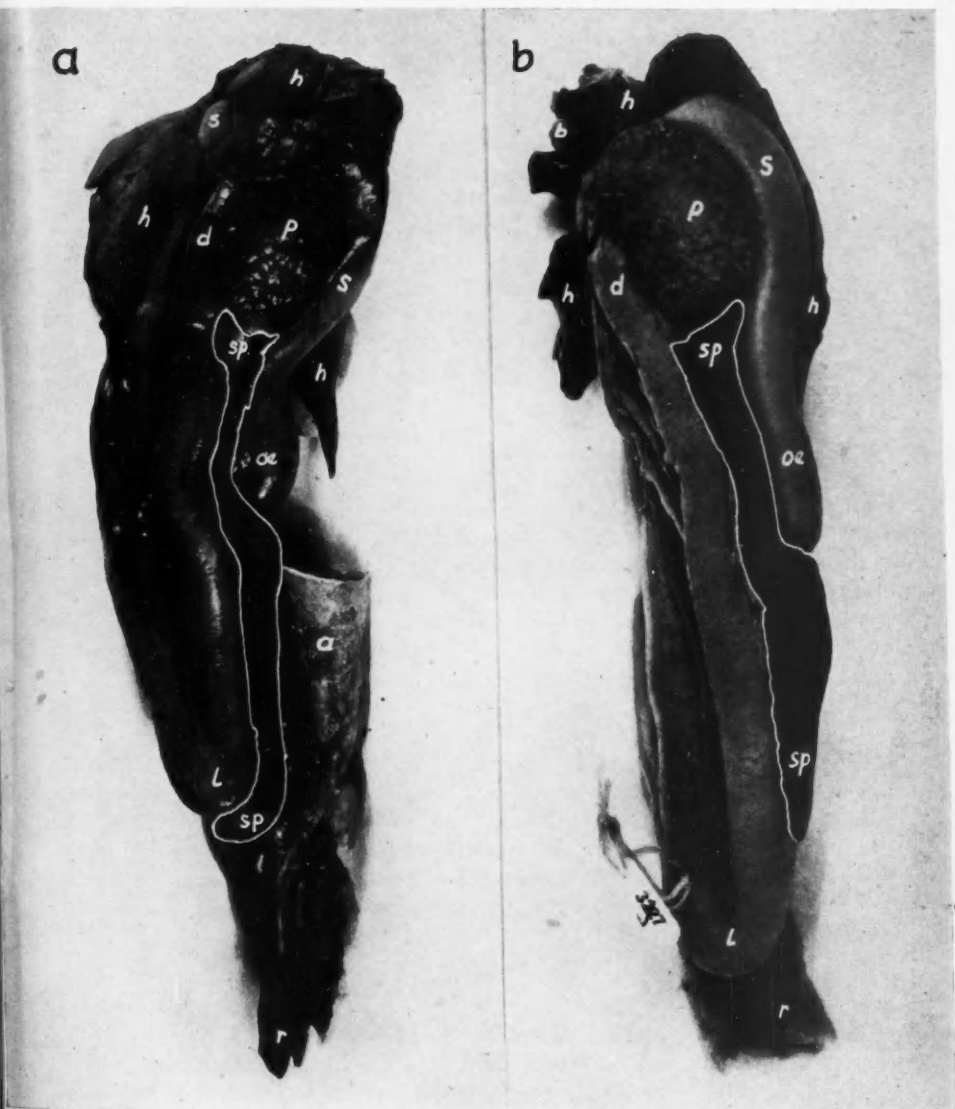


PLATE VII. Ventral view of the viscera of the two specimens of *A. oxyrhynchus de sotoi*. a—paratype (No. 59804); b—holotype (No. 59803); a—air-bladder; b—gall-bladder; d— duodenum; h—liver; l—loop of the small intestine; oe—oesophagus; p—pyloric apparatus; r—rectum; s—stomach; sp—spleen (outlined in white).

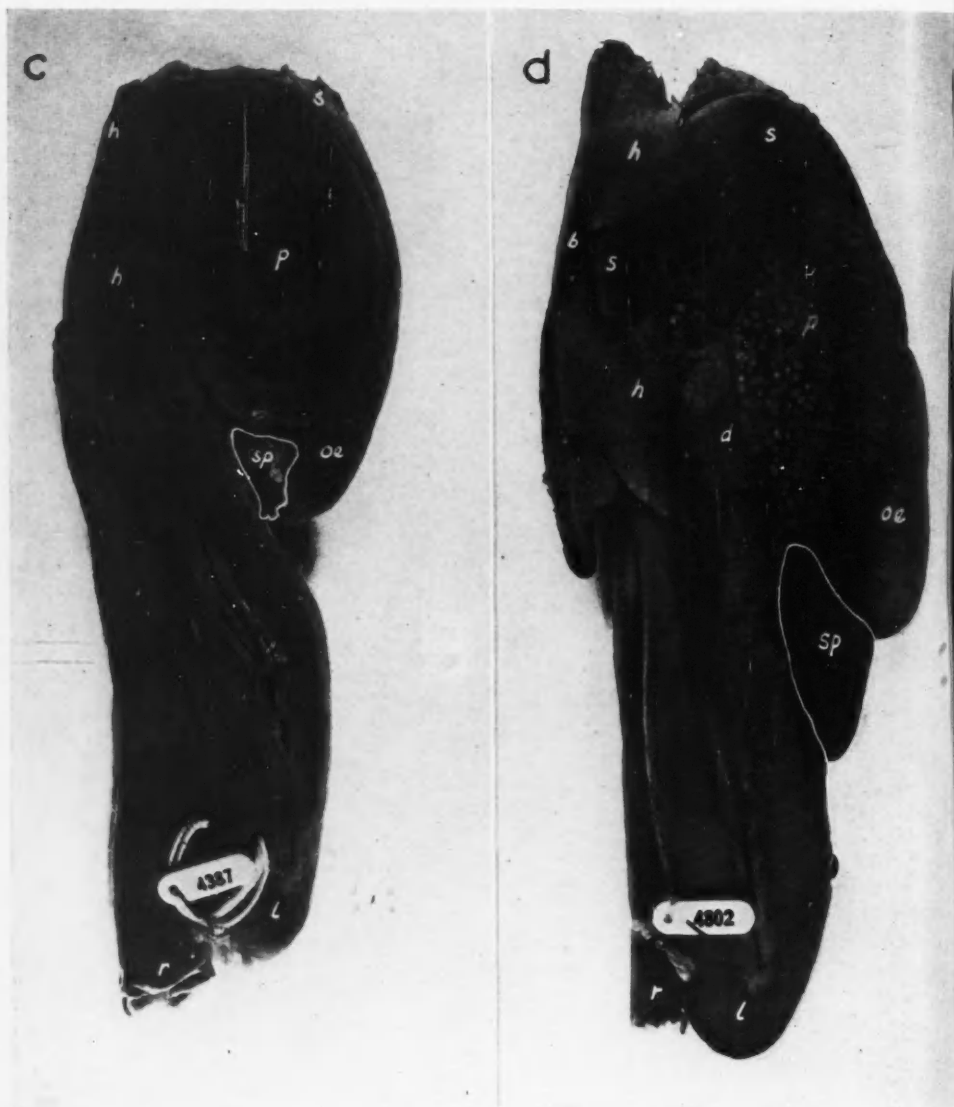


PLATE VIII. Ventral view of the viscera of two specimens of *A. oxyrhynchus oxyrhynchus*. c—from Florida (No. 35376); d—from Quebec (No. 876). For explanation see Plate VII.

DESCRIPTION

In order to make the comparison of the two subspecies of sea sturgeon more comprehensive, we shall deal with each character separately.

BODY PROPORTIONS

Details of body proportions, given in absolute and relative values, are found in Tables I-III. The method of measurements was that usually applied in taxonomic studies (see Vladykov and Greely, MS, 1955). It should be added, however, that in measuring the length of the snout (ML) and the post-orbital distance (pO), the membranous rim around the eye was included in both measurements. The length of the caudal peduncle (pc) was measured from the base of the last anal ray to the fork of the tail, that is, to the posterior extremity of the middle caudal rays. The width of the mouth (Be) was measured when it was closed, by using the greatest transverse distance of its slit, the thick lips included.

From the tables it is clearly seen that the Florida specimen (No. 35376), by its main body proportions, agrees very closely with fish from Quebec of corresponding size (No. 425). The principal differences between specimens of *de sotoi* and those of *oxyrhynchus* are first of all, in the length of head: in *de sotoi* it varies between 30.9–33.6% of the fork length, and only between 26.5–27.6% in *oxyrhynchus*. The snout and the postorbital distance are longer also in *de sotoi* and vary in percentage of the fork length respectively: 16.3–19.0, and 12.2–12.4; in *oxyrhynchus* the same parts are as follows: 11.6–15.3, and 9.0–11.6. The pectoral fins are also longer (15.5–16.3% of FL) in *de sotoi*, while in *oxyrhynchus* their fins vary only from 11.6–15.1% of fork length. The length of both pectoral and ventral fins, expressed in percentages of respective distances (P-V and V-A), is greater also in *de sotoi* than in *oxyrhynchus* (Table II).

In some characters, as the depths of body (H and h) and length of caudal peduncle (pc), the Florida specimen of subspecies *oxyrhynchus* is rather closer to *de sotoi* than to the individuals from Quebec. However, these characters are quite variable and hence not as important.

If we compare the principal body parts, expressed in averages of their absolute values, the difference between the southern subspecies (*de sotoi*) and the northern specimens is even more striking. Table III contains pertinent details.

SCUTES

In counting scutes we used those on left side of the fish and followed the same method in defining the first and last shields in each of the main rows, as was described by Vladykov and Beaulieu (1946). The first shield in the dorsal row corresponds to the occipital plate or *nuchale*, while the last is found just in front of an *enlarged fulcrum* at the beginning of the dorsal fin. The first shield of the lateral row, which borders on the posterior margin of the branchial cavity, is the *supracleithrum*. A small shield situated at the posterior extremity of the caudal peduncle, just before the remaining shields of the same row begin to rise

along the upper lobe of the caudal, is considered as the last shield of the lateral row.

Although the numbers of scutes in the main rows in *de sotoi* are somewhat smaller than in the Florida fish or Quebec specimens, the principal difference is in the shape of the scutes (Table IV and Plates I-IV).

(a) DORSAL SCUTES. In two specimens of *de sotoi*, 10 and 11 scutes were present in the dorsal row, while in northern specimens their numbers varied from 9 to 11.⁵ The shape of the scutes in the dorsal row is quite different in the two subspecies. In *oxyrhynchus* from Florida and Quebec they are rather oval, the length being greater than the width, while in *de sotoi* they are more square, with the length being much shorter than the width (Plates I, II). Moreover, the keel or carina on these scutes in *oxyrhynchus* is low, without a pronounced hook; in *de sotoi* there are typically two strong hooks on the keel of the scutes (Plate III). The measurements of the scutes are given in Table IV.

TABLE IV. Measurements in millimeters of scutes in sea sturgeon.

Subspecies	<i>A. oxyrhynchus de sotoi</i>				<i>A. oxyrhynchus oxyrhynchus</i>					
Locality	Gulf of Mexico				Florida		Quebec			
Catalogue Nos.	59803	59804			35376		876		877	
Dorsal scutes	Length	Width	Length	Width	Length	Width	Length	Width	Length	Width
1st	23	29	27	31	23	24	30	25	37	28
4th	24	32	31	35	23	25	28	24	33	27
6th	26	32	30	37	25	24	26	22	26	24
10th	20	26	23	29	23	21	26	19	28	18
Mean	23.3	29.8	27.8	33.5	23.5	23.5	27.5	22.5	31.0	24.3
Ventral scutes	Length	Height	Length	Height	Length	Height	Length	Height	Length	Height
1st	15	18	20	20	18	19	13	16	20	16
5th	20	24	23	27	20	17	15	19	18	19
10th	15	22	12	25	16	21	14	17	13	18
Mean	16.7	21.3	18.3	24.0	18.0	19.0	14.0	17.3	17.0	17.6

(b) LATERAL SCUTES. In two specimens of *de sotoi* 26 and 27 scutes were present in the lateral row, while in the northern specimens from 27 to 32 were present. The shape of these scutes in both subspecies is more or less the same, but their height in *de sotoi* is much greater than their length (Table IV). Moreover, in specimens from the Gulf of Mexico, there is a prominently developed keel on each scute, provided with a strong hook, behind which are present some additional sharp points. In northern specimens of comparable sizes neither keel nor hook is conspicuously noticeable (Plate IV).

(c) VENTRAL SCUTES. On the left side of two *de sotoi* specimens we counted 9 and 10 scutes in the ventral series; in comparison, three northern specimens

⁵For further details on the number of scutes in eastern American sturgeon species, see Vladikov and Beaulieu (1946).

had about the same number (10–11). The shape of the scutes in this row bears a certain resemblance to that of the dorsal scutes. Similarly, the length of the ventral scutes in *de sotoi* is much shorter than the width (Plate IV and Table IV). Moreover the last pair of ventral scutes, located in front of the ventral fins, are unusually large: in the holotype they almost touch one another along the median line, while in the paratype there is a narrow space between them. In northern specimens of *oxyrhynchus* these scutes are rather small, and typically well separated from one another (Plate VI).

(d) PRE-ANAL AND POST-DORSAL SCUTES. In specimens of *de sotoi*, these scutes are present in pairs as is the case for northern individuals as well (Plate VI). The principal difference is that in the Gulf of Mexico individuals the single last pre-anal scute, located immediately in front of the anal fin, is unusually large (Plate V).

DERMAL OSSIFICATION

Along the sides of sturgeon from the Gulf of Mexico, between regular rows of large scutes, there are present numerous small bony plates. In northern specimens, these dermal ossifications are much less developed, with perhaps the exception of the ventral surface (Plates V, VI).

GILL-RAKERS

In two specimens of *de sotoi*, the gill-rakers on the first branchial arch on the left side of the fish numbered 18 and 20, while in the northern sub-species they ranged from 20 to 25. For further details on gill-rakers of eastern American sturgeon species, see Vladykov and Beaulieu (1951).

INTERIOR ANATOMY

The most striking characteristic of the viscera in the two available specimens of *de sotoi* is the length of their spleen. In the paratype (Plate VII), it is narrow and extends from the pyloric apparatus past the lower end of the loop of the small intestine, while in the holotype it is somewhat shorter, but reaches far below the middle of the intestinal loop. The lengths of the spleen of these two specimens, expressed in percentage of fork lengths, are respectively 19 and 16. On the other hand, in subspecies *oxyrhynchus* (specimens from Florida and Quebec) it is a small, compact gland, typically not reaching the middle of the intestinal loop. In effect, in the Florida specimen it is equal to 3% of fork length and in 12 Quebec fish of comparable sizes it varies from 4% to 9% (average 6%). The length of the spleen, expressed in percentage of distance between the lower end of the pyloric apparatus and lower end of the intestinal loop, is 80–122% in *de sotoi*, while in the Florida fish it is 19% and in 12 Quebec specimens it ranges from 19 to 42% (average 31%).

Another peculiarity of the Gulf of Mexico specimens is the rather small size of their pyloric apparatus, the length of which is 6.6–7% of fork length, while in *oxyrhynchus* from Florida it is 11% and in 12 Quebec fish from 7 to 10% (average 8%). The length of the spleen in percentage of the length of pyloric apparatus

is 238–274% in *de sotoi*, 30% in the Florida fish, and 49–98% (average 69) in 12 Quebec specimens.

OCCURRENCE

Our two specimens of *de sotoi* were obtained in the Gulf of Mexico, at the mouth of Singing River, off Gautier in the Mississippi Sound. While at Gainesville, Florida, the present author, thanks to Dr. E. G. Kilby, had the opportunity to examine briefly fish collections of the University of Florida. There were 2 sea sturgeon taken at Cedar Keys, and 1 caught in the Suwannee River, both localities in Florida on the Gulf of Mexico side. Even a superficial examination convinced us that they also belonged to the *de sotoi* subspecies.

All records of sea sturgeon from the Gulf of Mexico, including the Mississippi Delta, probably should be considered as *de sotoi*. In effect, a photograph of a large sturgeon, taken near the mouth of the Mississippi River, published in Gowanloch's *Fishes and Fishing in Louisiana* (1933, p. 408) can be identified as *de sotoi* by its broad and strongly developed scutes.

There have been reported occasional captures of sea sturgeon in Bermuda (Beebe and Tee-Van, 1933, p. 32) and even in French Guiana.⁶ The latter specimen, collected by Frère in 1830 from the Oyapock River, known as "la Cayenne", was described by Duméril (1867, p. 161) as a new species, *A. cayennensis*. It is now stuffed and kept in good condition in the Paris Museum National d'Histoire Naturelle. Thanks to Dr. L. Bertin, the present author had the opportunity to examine in Paris, in 1950, the Guiana specimen, with a total length of 740 mm., and identify it as an *A. oxyrhynchus*, with strongly developed dermal ossifications. Thus we consider that all the above southern stragglers could be easily of the *de sotoi* subspecies, as they, no doubt, are more accustomed to higher temperatures.

The northern subspecies *oxyrhynchus* occurs along the western Atlantic coast, from Florida to Quebec. The relationship between two subspecies of *A. oxyrhynchus* is analogous to that found in the chase of the shads, *Alosa sapidissima* and *Alosa alabamæ*, of the Atlantic and Gulf of Mexico coasts, respectively. Rivas (1954, p. 504) wrote in this connection: "These two very closely related, vicarious species seem to have evolved when the original ancestral population, continuous along the south coast of the United States, was split by the emergence of peninsular Florida. Neither *Alosa sapidissima* nor *A. alabamæ* occur around south Florida."

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⁶Bertin (1940, pp. 248–249) considered the Guiana specimen as a possible hybrid *A. sturio* × *A. brevirostris*.

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The Cirripede Crustacea of the Hudson Strait Region, Canadian Eastern Arctic^{1, 2}

"CALANUS" SERIES NO. 7

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ABSTRACT

The distribution, bathymetrical occurrence and spawning periods of three widely distributed arctic-boreal species of barnacles, *Balanus balanoides*, *B. balanus* and *B. crenatus*, are given from Ungava Bay, Frobisher Bay, Cumberland Sound and Hudson Strait.

INTRODUCTION

THE present account provides a station list of barnacle species taken by the *Calanus* expeditions of 1947-52 in the waters of Hudson Strait and contiguous areas. The station lists, with place names, bathymetrical records and maps, are given by Dunbar and Grainger (1952) and Grainger (1954). The collection includes littoral and benthic forms taken by hand along the shore and by dredges and nets along the bottom.

The diagnostic features of the species in the present material show little variation from those in published descriptions. The wall plates (parietes) are notoriously variable in shape and external sculpturing and on this account the external morphology is of little taxonomic value. Three main *ecophenotypes* or growth forms were noted in *Balanus*: the typically conical shape of isolated specimens, the columnar form of specimens closely crowded in the same plane, and the "curved" form of individuals growing one upon the other.

The dearth of published information on the spawning periods of barnacles in arctic and subarctic regions has prompted the present analysis of the ovigerous condition of adult barnacles and seasonal occurrence of the newly attached and metamorphosed larvae (basal diam. < 3 mm.). The findings are consistent with the known seasonal occurrence of the larvae obtained in plankton hauls of the *Calanus* expeditions (H. Barnes, personal communication), and in eastern and western Greenland (Madsen, 1936; Thorson, 1936), and with spawning periods in Labrador (Bousfield, 1954).

The author is much indebted to Dr. M. J. Dunbar, Dr. E. H. Grainger and Mr. D. V. Ellis for providing material and field notes used in this report.

¹Received for publication, March 24, 1955.

²Contribution from the National Museum of Canada.

SYNOPSIS OF THE SPECIES

SUBORDER BALANOMORPHA

FAMILY BALANIDAE

(i) *Balanus (Semibalanus) balanoides* (L.)

More than 320 adult specimens and many newly metamorphosed young barnacles were taken at 24 intertidal and 3 benthic stations in Ungava Bay and Hudson Strait, 1947-50, Frobisher Bay, 1951, and Cumberland Sound, 1952:

- 1947: Stn. 1A (June 24)—32 spec.; Stn. 5 (June 29)—17 spec.; Stn. 8 (July 5)—15 spec.
 1948: Stn. 65 (July 12)—7 spec.
 1949: Stn. 107A (July 9)—10 spec.; Stn. 112 (July 18)—19 spec.; Stn. 123 (Aug. 10)—22 spec.
 1950: Stn. 201A (June 27)—4 spec.; Stn. 203 (July 8) 30 m. dredge—1 spec.; Stn. 204 (July 9)—15 spec.; Stn. 205 (July 14)—4 spec.; Stn. 208 (July 21)—wall frags.; Stn. 212 (July 21)—6 spec.; Stn. 217 (July 30)—8 spec.; Stn. 224A (Aug. 18)—8 spec., 22 newly metamorph.; Stn. 227 (Aug. 18)—70 spec., 4 newly metamorph.; 1 attached cyprid; Stn. 227 (Aug. 18)—1 spec.; Stn. 229 (Aug. 26)—6 spec., 2 newly metamorph.; Stn. 229 (Aug. 28)—6 spec., 6 newly metamorph.; Stn. 231 (Aug. 27) 63-75 m. dredge—3 spec.; Stn. 235 (Sept. 1)—11 spec.
 1951: Stn. 310 (July 29)—2 spec.; Stn. 316 (Aug. 8)—11 spec.; Stn. 330 (Aug. 21)—2 spec.
 1952: Stn. 406 (July 27) 25 fath. dredge—1 spec., frags., 3 newly metamorph.; Stn. 413 (Aug. 5)—4 spec.; Stn. 418 (Aug. 14)—6 specimens.

DISTRIBUTION: "From latitude 66°34' north in the Atlantic Ocean to the ocean coast of France and to Delaware Bay; in the Pacific—from Unalaska to Stitka" (Pilsbry, 1916). The species is known from Greenland south of latitude 66°N. on the east coast and 73°N. on the west coast, (Madsen, 1936), southern Baffin Island (Ellis, unpublished), Labrador (Rathbun, 1910), and the entire Atlantic coast of Canada (Bousfield, 1954).

From the northeastern part of Hudson Bay the following material in the collections of the Royal Ontario Museum of Zoology and Palaeontology has been examined:

Nottingham Island; inlet at base "B" on south end, "Loubyrne" expedition, Aug. 6, 1927. F. Johansen coll.—12 specimens.

The occurrence of *B. balanoides* at depths of 30, 46 and 63 metres (Stns. 203, 406 and 231) in the Hudson Strait region is in accord with the subtidal bathymetrical distribution of the species in the Gulf of Maine (Bousfield, 1954).

(ii) *Balanus balanus* (L.)

Syn: *Balanus porcatus* Da Costa

More than 225 adult specimens and numerous newly metamorphosed young were obtained at 24 benthic stations in depths ranging from 27 m.—300 m. as follows:

- 1947: Stn. 13 (July 13)—old wall frags.; Stn. 18 (July 17)—1 spec. parietes only, frags.; Stn. 25 (July 19)—3 spec., frags.; Stn. 27 (July 19)—19 spec., 1 newly metamorph.; Stn. 28 (July 19)—2 spec.; Stn. 30 (July 20)—10 spec., 2 newly metamorph.; Stn. 33 (Aug. 8)—37 spec., numerous newly metamorph., 1 cyprid; Stn. 33 (Aug. 10)—8 spec.
 1949: Stn. 102 (June 30)—2 spec., 2 newly metamorph.; Stn. 103 (July 6)—9 spec., 3 newly metamorph.; Stn. 126 (Aug. 23)—2 spec.

- 1950: Stn. 203 (July 8)—5 spec., numerous newly metamorph.; Stn. 206—(July 15)—3 frags.; Stn. 208A (July 20)—8 spec., 6 frags.; Stn. 222 (Aug. 3)—4 spec., 1 frag., a few newly metamorph.; Stn. 226 (Aug. 13)—more than 100 spec., 10 newly metamorph.
 1951: Stn. 317 (Aug. 9)—2 spec. (1 very large—4.0 cm. basal diam.); Stn. 318 (Aug. 9)—1 frag.; Stn. 322 (Aug. 12)—4 spec., 14 newly metamorph.; Stn. 331 (Aug. 22)—9 spec., a few newly metamorph.; Stn. 333 (Aug. 24)—8 spec., 35 newly metamorph.; Stn. 334 (Aug. 24)—2 frags.
 1952: Stn. 406 (July 22)—1 spec., frags. only; Stn. 413 (Aug. 5)—1 large spec., parietes only.

DISTRIBUTION: "Arctic and North Atlantic Ocean, from 80°N. Latitude, Franz Joseph Archipelago, to the English Channel, and in America south to Nantucket and Long Island Sound. Not located off the Grand Banks of Newfoundland." (Pilsbry, 1916). North Pacific south to Puget Sound (Cornwall, 1954). Known from both east and west coasts of Greenland (Weltner, 1900; Thorson, 1936), eastern Baffin Island (Ellis, unpublished), Labrador (Rathbun, 1910) and the Atlantic coast of Canada (Bousfield, 1954).

In the collections of the National Museum of Canada are specimens, identified by H. A. Pilsbry, from the following localities in Arctic Canada:

- Hudson Strait: Ashe Inlet, Big Island, 1884, R. Bell coll.—several dried specimens.
 Dolphin and Union Strait, N.W.T., Canadian Arctic Expedition Stn. 43c, 10–75 fath., Sept., 1915, F. Johansen coll.—fragments (dried).
Ibid., Stn. 43a, 50 fath., fragments (dried).
 Bernard Harbour, N.W.T., C.A.E. Stn. 37p, washed up on beach, Oct., 1914, F. Johansen coll.—fragments (dried).

B. balanus was taken in depths from 15–200 metres, mainly 30–100 metres. This species, occurring in 24 of 30 benthic stations at which barnacles were taken, appears to be more common and more abundant than *B. crenatus* in the Hudson Strait region.

(iii) *Balanus crenatus* Bruguière

Approximately 225 adult specimens and many newly metamorphosed young were obtained at 14 benthic and 2 intertidal stations, in depths ranging from 0 to 252 m., as follows:

- 1947: Stn. 18 (July 17)—wall frags. only; Stn. 33 (Aug. 8)—11 spec.; Stn. 33 (Aug. 10)—138 spec., a few newly metamorph.; Stn. 48 (Aug. 23)—1 spec.
 1948: Stn. 58 (July 28)—2 spec., some newly metamorph.; Stn. 65 (July 12) intertidal—4 specs.
 1949: Stn. 103 (July 6)—3 frags.; Stn. 126 (Aug. 23)—1 spec.
 1950: Stn. 201c (June 29)—30 spec., a few newly metamorph.; Stn. 208A (July 20)—2 frags.; Stn. 208 (July 21) intertidal—1 frag.; Stn. 210 (July 11)—1 spec.; Stn. 226 (Aug. 13)—30 spec., 13 newly metamorph.
 1951: Stn. 321 (Aug. 11)—numerous wall frags. columnar type; Stn. 322 (Aug. 12)—3 specs.
 1952: Stn. 406 (July 22)—3 newly metamorph.

DISTRIBUTION: "Arctic ocean; North Atlantic south to Long Island Sound; Bering Sea and North Pacific south to Santa Barbara, California, and Northern Japan" (Pilsbry, 1916). Known from Greenland (Weltner, 1900), Labrador (Rathbun, 1910) and the entire Atlantic coast of Canada (Bousfield, 1954).

In the National Museum of Canada are specimens, identified by H. A. Pilsbry, from two localities in Arctic Canada:

Hudson Strait, Ashe Inlet, Big Island, 1884, R. Bell coll.—several (dried) specimens.

Hudson Bay, east side, mouth of Povungnituk R., 1898, A. P. Low coll.—several (dried) specimens.

B. crenatus was taken from the tide lines down to 200 metres, mainly about 30 m. As few dredgings were made in depths of less than 15 m., no reliable estimate of abundance with depth can be made from the present material. However, in this subarctic region *B. crenatus* apparently inhabits waters that are somewhat shallower and presumably warmer than those of *Balanus balanus*.

SPAWNING SEASONS

The present material provides clues to the times of spawning of adults and occurrence of barnacle larvae in the plankton in the Hudson Strait region. Because of complicating factors, however, a clear picture of the time of spawning, particularly of *Balanus balanoides*, is difficult to derive. The number of samples is small, and the samples were taken from widely separated localities and various levels of the littoral and sublittoral zones having different water temperatures and different degrees of exposure to frost, ice and wave action. These factors are thought to be important in determining the development and release of the eggs. Also, the lots represent but three months of the year (mid-June to mid-September), a time when few or no eggs and larvae are present either in the ovaries or in the ovigerous lamellae. Moreover the samples were taken in different years when, at corresponding dates, ecological conditions were different.

The following notes were made on the barnacle material:

Balanus balanoides

Ovaries were thin or very thin in most specimens taken during June and early July, thickening in late July and early August, and thick and yellowish in late August and early September.

Segmenting eggs were observed in three specimens only, taken July 9/49, July 20/50 and Aug. 22/51. Nauplii were found in specimens taken June 24/47, July 9/49, July 9/50 and July 29/50.

Nauplii and segmenting eggs were found in a single specimen from Stn. 6A, Frobisher Bay, D. V. Ellis coll., June 19–21, 1952.

Newly attached cyprid larvae and newly metamorphosed young barnacles (basal diam. less than 3 mm.) occurred on Aug. 18/50; the latter also on Aug. 26 and Aug. 28, 1950.

In this species spawning normally takes place only once per year, commencing in the second year. From the above observations it may be deduced that the eggs develop in the ovaries during the months of July and August and are probably deposited and fertilized in the ovigerous lamellae in September and October. The eggs develop to the nauplius stage during the long winter period, and spawning takes place mainly in June and early July, when ice first dis-

appears from the shore areas. Attachment of cyprids takes place chiefly in July and August.

Balanus balanus

Although several year classes (including the non-spawning first-year class) have been examined, none containing eggs or developing nauplii was observed. Ovaries were thin in late June and early July, somewhat thicker in late July and early August, and moderately thick in late August.

Newly metamorphosed young barnacles occurred in lots taken June 30/49, July 6/49, July 8/50, July 18/47, Aug. 3/50, Aug. 8/47, Aug. 12/51, Aug. 13/50, Aug. 22/51 and Aug. 24/51, and a cyprid on Aug. 8/47.

The reproductive cycle is much as in *B. balanoides*, but spawning may take place slightly earlier in the season. The eggs are probably deposited and fertilized in September, develop to the nauplius stage during the winter, and are liberated into the water during late May, June and early July. Attachment of cyprids commences about the end of June and continues through July into August.

In a study of 15 specimens of *B. balanus* from Scoresby Sound, Northeast Greenland (lat. 70°N.), Thorson (1936) found none containing eggs. Nauplii were taken in the plankton on June 17 and July 11, with most occurring later. The larval sequence in *B. balanus* is complete (6 nauplius stages and a cyprid stage), but under abnormally poor breeding conditions the larvae may be retained in the mantle cavity until reaching the cyprid stage of development.

Balanus crenatus

Ovaries thin and watery in June and July; thickening in August. One lot (Aug. 23, 1947) with thick ovaries.

Segmenting eggs were found in a single specimen at Stn. 126, 70-91 m., Aug. 23/49. Nauplius stage 1 occurred in two specimens taken Aug. 11/47 and Aug. 13/50.

A newly attached cyprid was taken Aug. 13/50, and newly metamorphosed barnacles on July 22/52, July 28/48, Aug. 11/47 and Aug. 13/50.

In material from Frobisher Bay and Cumberland Sound collected in 1952 by D. V. Ellis, nauplii and segmenting eggs in many adults and newly metamorphosed young were taken June 22, and the former occurred in one adult taken July 29-Aug. 1.

During July and August the ovaries become thick and eggs are probably deposited in September and October. Spawning takes place in first-year individuals of this species. Nauplii are released in June and July; those from deep-lying barnacles in August. Cyprids attach mainly in late June, July and August. The normal reproductive cycle contains two broods per year near the southern limit of distribution. Here, near its northern limit, more than one brood per year is unlikely. The spawning season appears to be slightly later than that of *Balanus balanus*.

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The Inconnu (*Stenodus leucichthys mackenziei*) in Great Slave Lake and Adjoining Waters^{1, 2}

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ABSTRACT

Material for this study was gathered by field parties of the Fisheries Research Board in the summers of 1944, 1945 and 1946. A description of the subspecies is given, based on measurements of 26 specimens. The distribution of *Stenodus* in Great Slave Lake, and in northern North America is outlined. The rate of growth was determined from an examination of scale samples from 298 fish, and it was found that the inconnu has a rapid growth rate, even in this highly oligotrophic lake. Inconnu spawn mainly in the rivers which enter Great Slave Lake from the Mackenzie Lowlands. The upstream run apparently occupies most of the summer but evidence is presented which indicates a major movement in late August. The post-spawning, downstream run takes place in late September or early October. Residents take advantage of it to put up inconnu for winter dog feed. The food of young inconnu in the spawning streams was found to be mainly invertebrates, whereas in Great Slave Lake the species is almost entirely piscivorous. A list of parasites is given, among which *Triaenophorus crassus* is considered of major importance. The rate of infestation with the larvae of this worm is high—88 per cent of 49 fish examined, at a rate of 64 cysts per 100 pounds. At present the major use of the inconnu is in the domestic fishery where it serves local trappers, and others, as dog feed.

INTRODUCTION

Previous published accounts of the inconnu, *Stenodus leucichthys mackenziei* Richardson, have dealt mainly with its distribution and have produced few authenticated details of its life history. The earliest record of *Stenodus* in Great Slave Lake is that of Hearne (1795) who took specimens in the east arm in 1772. Mackenzie (1801) reported its occurrence in the river which now bears his name. Richardson's description, based on specimens from the Mackenzie valley, was published in 1823. Melville (1914) reviewed earlier work and included some material relating to the natural history of the species. Additional information, especially on the taxonomic aspects, was presented by Dymond (1943).

An opportunity to carry out a more detailed investigation of the ecology and economic importance of *Stenodus* in Great Slave Lake arose when the Fisheries Research Board of Canada began a survey of the biology and fisheries possibilities of the lake in 1944. As a member of the survey party, the writer was able to make special observations in the field in the summer of 1946. D. S.

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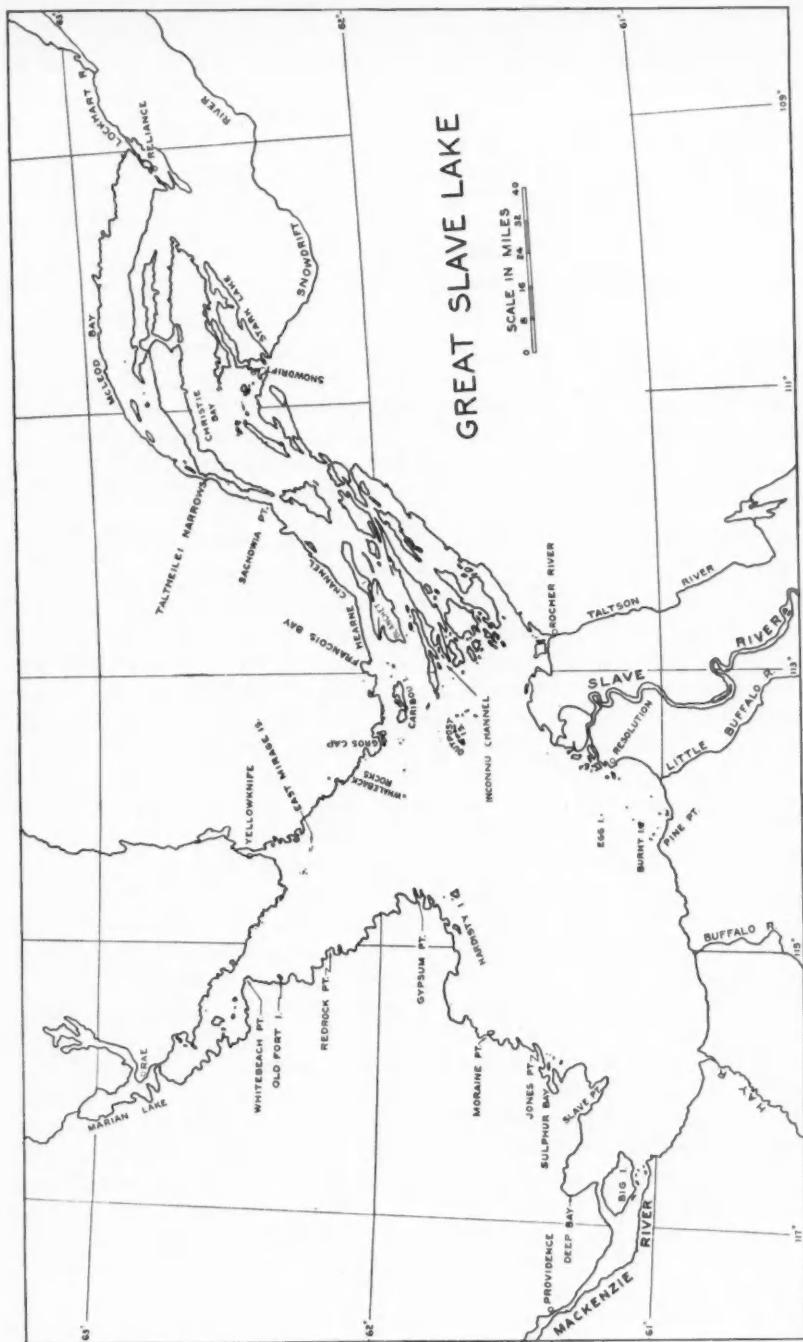


Figure 1. Map of Great Slave Lake showing places mentioned in the text.

Rawson, Director of the project, made available all pertinent records of the two previous summers.

During a subsequent period of residence in the Northwest Territories, additional information has come to hand through personal observation and conversations with government officials, trappers, traders, missionaries and others who have first hand knowledge of the inconnu.

ACKNOWLEDGMENTS

It is a pleasure to acknowledge the help received from several sources. D. S. Rawson, Department of Biology, University of Saskatchewan made the field and laboratory work possible, and his interest, guidance and constructive criticisms have been of inestimable value. Special thanks are also due W. A. Kennedy, Fisheries Research Board of Canada, for suggestions and criticisms and for permitting the use of certain data. R. B. Miller, University of Alberta, identified the parasites collected during the course of the study. The National Research Council of Canada provided assistance in the form of a bursary.

GEOGRAPHICAL AND PHYSICAL FEATURES OF GREAT SLAVE LAKE

Great Slave Lake (Fig. 1) lies in the Northwest Territories, extending approximately from 61° to 63° north latitude and from 109° to 117° west longitude. It is fifth in order of size of North American lakes with an area of 10,600 square miles. Its shape and many of its physical features are conditioned to an important degree by its position astride the edge of the Precambrian Shield. Thus, the northeast shore of the north arm and the entire east arm are within the Shield and have highly irregular, precipitous margins, while the remainder of the lake lies in the broad alluvial plain known as the Mackenzie Lowlands and has gently sloping, sandy or boulder-strewn beaches. The rivers flowing into the lake from the Precambrian formation are cold, clear and frequently interrupted by spectacular falls and rapids. Those entering from the south are, on the other hand, shallow, gently flowing and laden with silt.

The main body of the lake is of moderate depth, the maximum being 535 feet. The long north arm is shallow, while the east arm is extremely deep. A portion of Christie Bay in the east arm exceeds 2,000 feet in depth.

The Slave, Big Buffalo, Taltson and Hay Rivers are of major importance in the present study. They have in common, besides their northerly direction of flow, a heavy load of silt and long stretches free from rapids or falls. The Taltson is blocked by falls 25 miles from its mouth, the Hay has falls at mile 48 and the Slave is blocked by rapids at Fort Smith, some 200 river miles above the lake. The Big Buffalo is navigable with canoes to its source in Buffalo Lake, though its course is interrupted by many shallow rapids. Most of the streams which feed Buffalo Lake have their origins in the Caribou Hills. Their upper reaches have many rapids and falls, but about 20 miles from the lake they enter a flat plain and maintain a placid course with little current.

The physical limnology, fish and bottom fauna of the lake have been described by Rawson (1950, 1951 and 1953).

TAXONOMY

MEASUREMENTS AND COUNTS OF BODY PARTS

Twenty-six fresh specimens of inconnu were measured during the summer of 1946, following the method of Koelz (1929). Tables I and II contain a summary of these measurements along with comparative material from the Slave River (Dymond, 1943) and Teslin Lake, northern British Columbia and Yukon Territory (Clemens, 1944). Table I includes only mature fish, 60 cm. or more in standard length. Proportionate measurements are used throughout.

DESCRIPTION

A description of the distinguishing structural features of the inconnu was given by Dymond. The following description is modified where necessitated by the observations of the writer, especially those observations set forth in Tables I and II. Head long (one-quarter of standard length), and pointed; lower jaw longer than upper and slightly hooked; maxillary slightly more than one-third of head length, reaching to posterior margin of pupil; greatest antero-posterior

TABLE I. Proportionate measurements of *Stenodus* from Great Slave Lake, 1946 (18 specimens); Slave River, Dymond, 1943 (11 specimens); Teslin Lake, Clemens, 1944 (6 specimens).

	Great Slave Lake		Slave River		Teslin Lake	
	Mean	Extremes	Mean	Extremes	Mean	Extremes
Head length	25.6	23.6-28.1	26.7	25.9-27.7	26.8	24.6-28.6
Head depth	13.2	12.2-15.5	15.3	14.5-15.7	14.0	12.0-15.8
Eye	3.4	3.2- 4.1	3.5	3.2- 3.8	3.4	2.8- 4.2
Snout	4.9	4.2- 5.9	6.0	5.7- 6.5	6.2	5.3- 7.2
Interorbital	4.7	4.2- 5.5	4.8	4.4- 5.2	4.8	4.4- 5.2
Maxillary	9.1	7.5-10.5	9.4	9.0- 9.8	9.5	8.5-10.7
Body depth	21.5	19.5-22.6	21.3	20.0-23.5		
Body width	13.1	9.9-15.5	13.2	12.0-14.9		
Caudal peduncle height	10.0	9.1-11.3	11.0	10.0-11.6	9.4	9.0-10.6
Caudal peduncle width	6.8	6.1- 7.5	7.1	6.5- 7.8	6.5	6.0- 7.0
Dors. fin height	15.2	9.8-16.8	15.0	13.3-16.6	13.6	13.1-14.2
Dors. fin base	11.5	9.6-12.8	11.3	10.4-12.3	10.6	10.0-11.2
Anal fin height	12.7	10.6-14.5	12.5	11.7-13.8	11.5	10.7-12.6
Anal fin base	11.8	10.6-12.7	11.8	11.0-13.0	11.1	10.4-11.7
Pectoral length	15.9	14.5-17.0	16.6	16.1-17.6	15.1	14.0-15.9
Ventral length	14.0	13.1-15.6	15.2	13.8-16.2	12.9	12.0-13.4

TABLE II. Counts of body parts of *Stenodus* from Great Slave Lake, 1946 (26 specimens); from Slave River (by Dymond, 1943); and from Teslin Lake (by Clemens, 1944).

	Great Slave Lake			Slave River			Teslin Lake		
	Mean	Mode	Extremes	Mean	Mode	Extremes	Mean	Mode	Extremes
Scales	97.9 ^a	97	92-107	103	...	100-107	98.7	...	90-105
Gill rakers	7.4+15.7	7+16	6+14-9+18	7+14	21	7+12-8+15	20.1	21	19-22
Branchiostegals	10.2	10	9-11	10.6	...	10-12	10.5	...	10-11
Dorsal fin rays	12+2.4	2+12	1+11-3+16	13.6	14	12-15	14.3	14	13-15
Anal fin rays	14.5+2	2+14	3+13-2+17	15.6	16	15-16	16.4	17	15-18
Vertebrae	64.3+2.6 ^b	65+3	62+2-67+2

^aBased on 25 specimens. One badly rubbed individual not included.

^bThree specimens had fusion of vertebrae, so this average is based on 23 specimens.

diameter of eye about three-quarters of the length of the snout; snout approximately equal to inter-orbital; nostrils with 2 flaps; branchiostegals 10, occasionally 11, rarely 9 or 12; gill rakers of moderate length, stiff and bony, number on first arch most commonly 7 plus 16; very small teeth on palatine, vomer, tongue, premaxillary, head of maxillary and anteriorly on lower jaw. Body long and slender (depth about one-fifth of standard length), uniform silvery colour, somewhat darker above (more noticeable in young specimens); dorsal fin with 12 fully developed rays preceded by two or three shorter ones, slightly higher than long, posterior margin dusky; anal fin immaculate with 14 or 15 developed rays preceded by two or three shorter ones, its base nearly equal to its height; pectorals and pelvics well developed, immaculate; caudal edged with black; scales in lateral line to end of caudal peduncle 98 (90-107); vertebrae 65 to end of caudal peduncle plus two or three rudimentary.

NOMENCLATURE

Richardson (1823) accorded the inconnu specific rank and named it *Stenodus mackenzii* which is emended to *mackenziei* in accordance with the Paris decisions of the International Commission. The name still stands though Melville (1914), Dymond (1943), and others quoted by Dymond have suggested the synonymy of *Stenodus mackenziei* and *Stenodus leucichthys*.

Descriptions of *S. leucichthys*, the asiatic form, are in Russian and thus not easily obtainable. The gill raker count is reported to be 22 with a range of 19 to 25 which agrees almost exactly with the values in Table II. Dymond considers that the gill raker count is the most stable character of the coregonine fishes of northwestern America. This evidence, therefore, strengthens the contention of the authors quoted that *mackenziei* should be considered a subspecies of *Stenodus leucichthys*.

The series of scale counts obtained by the writer (Table II) does not support Dymond's suggestion of racial differences in American *Stenodus*. The counts of Mackenzie River specimens quoted by Dymond fall well within the range of variation of the Slave Lake specimens.

DISTRIBUTION

The inconnu appears to reach maximum abundance in two localities in Great Slave Lake. The more extensive area lies in the shallow, heavily silted water off the south shore from the Slave River Delta to the source of the Mackenzie. The other, much smaller locality is at the western approach to Inconnu Channel, in the angle between Simpson and Wilson Islands. Inconnu are present but less abundant along the west shore, in the north arm and in the Gros Cap area. They are seldom found in the deeper portions of the main body of the lake and have been taken in MacLeod and Christie Bays only on rare occasions. Depth seems to be the main controlling factor. In a great many settings of test nets, at all depths, inconnu were seldom taken deeper than 100 feet (30 metres).

Stenodus is found up the Slave River as far as the rapids at Fort Smith, and

down the Mackenzie to its mouth. Spawning runs occur in the lower tributaries of the Mackenzie such as the Peel and the Arctic Red Rivers. The Anderson River, 150 miles east of the Mackenzie, marks the eastern limit of the range of the inconnu. It is found in all the rivers westward from the Mackenzie to the west coast of Alaska. The western limit is unknown, nor is there information concerning a possible zone of intergradation with *Stenodus leucichthys nelma*, the Asiatic form.

RATE OF GROWTH

MATERIALS AND METHODS

During the summers of 1944 and 1945, scale samples were taken only from a representative series of the inconnu taken in the test nets—standard gangs composed of 50 yards each of 1½-, 2-, 3-, 4½-, 5-, 5½-inch stretched mesh. In 1946 scales were saved from all inconnu taken, except a few badly rubbed immature specimens, and, in addition, from about 350 fish taken in commercial gear (5½-inch mesh). Since the commercial fish were fairly uniform in size, only a small series was mounted for study. Altogether, scales from 326 fish were studied, and ages were assigned to 298.

Scales were cleaned of mucus in dilute potassium hydroxide, washed in dilute acetic acid, rubbed gently between thumb and forefinger, dried between filter papers and mounted in glycerine jelly. The image of the scales was projected at a magnification of about 21 diameters, the annuli were counted and the distances between successive annuli measured. All pertinent data for each fish were recorded on index cards.

RESULTS

The rate of growth in length of the inconnu in the sample is summarized in Table III and shown graphically in Figure 2. The standard length is used throughout. The inconnu grows much faster than the common whitefish (Kennedy, 1953) and slightly faster than the lake trout (Kennedy, personal communication). A suggested explanation is that the inconnu is an arctic fish at the

TABLE III. Mean standard length and weight of each age group in a sample of inconnu from Great Slave Lake.

Age	Mean length	Standard deviation	Mean weight	Standard deviation
	cm.	cm.	lb.	lb.
1	14.6	3.08	0.12	...
2	24.7	3.02	0.44	0.22
3	31.2	6.06	0.87	0.49
4	40.3	3.60	1.62	0.41
5	47.3	3.60	3.00	1.22
6	52.9	5.24	4.36	1.27
7	57.2	5.35	5.62	1.51
8	61.0	4.42	7.13	1.70
9	65.7	4.26	8.31	1.75
10	68.8	4.45	9.75	1.94
11	72.7	3.86	11.05	2.06

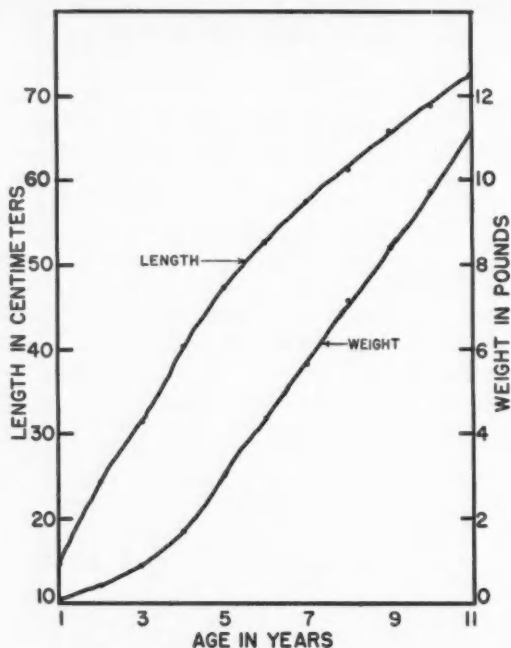


FIGURE 2. Curves showing rate of growth in standard length (cm.) and weight (pounds) of a sample of 298 inconnu.

southern limits of its range, whereas the other species are temperate ones approaching their northern limits.

The annual increment of growth for each fish in the sample was calculated by means of the body-scale relationship. Then the average annual increment of the whole sample was determined and plotted. The resulting curve (Fig. 3) showed an apparent acceleration in the growth rate in the fourth year of life. The possible significance of this observation is discussed in a later section.

The rate of growth in weight is also shown in Table III and Figure 2. It is apparent that the inconnu increase only slowly in weight for the first four years, then more rapidly until at least the eleventh year. There are too few specimens older than eleven to permit a continuation of this curve.

Close examination revealed that new circuli were seldom present on scales of fish caught earlier than the last week in June. An annulus was noted on almost all the scales from fish caught during the first week in September. Scale growth, therefore, takes place mainly in the months of July and August. Maximum body growth is assumed to take place at this time also. The data also suggest that older fish, in general, have a shorter growing season.

No sexual difference in the rate of growth in length could be detected. In

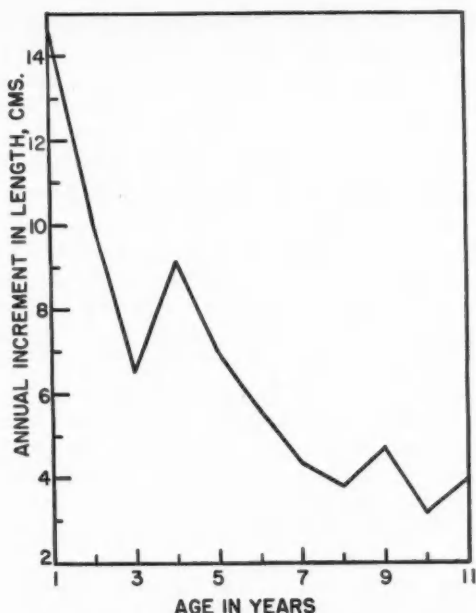


FIGURE 3. Average annual increment of growth in standard length of a sample of 298 inconnu, showing acceleration of growth rate in the fourth year.

weight, particularly in the upper age groups, there was a tendency for females to exceed males. This is to be expected in view of the larger size of the female gonad.

SPAWNING AND MIGRATION

Residents of the Great Slave Lake area have long known about the migratory habits of the inconnu and have made use of this knowledge to fulfil their annual needs for dog feed. The fish return to Great Slave Lake from the spawning grounds in large numbers at a definite brief period each autumn and are then easily taken and preserved for winter use. The major runs occur on the Big Buffalo and Taltson Rivers, with smaller runs on the Slave, Little Buffalo and Hay Rivers.

According to the testimony of several long-time residents of the area, the run on Big Buffalo River takes place between September 27 and October 12. Others have reported that the Taltson River run usually precedes the Big Buffalo run by three or four days.

The run on the Big Buffalo was studied for the Fisheries Research Board between September 29 and October 12, 1945, by Larkin (MS. 1945). He found small numbers of ripe inconnu of both sexes at the mouth of the Big Buffalo

right up to the commencement of the downstream run. From an examination of 127 fish taken at this time, he was able to determine the size of the fish at maturity. Some males mature at a standard length of 55 cm. About 20 per cent of males between 55.0 and 59.5 cm. were mature; about 70 per cent between 60.0 and 64.5 cm.; and 90 per cent between 65.0 and 69.5 cm. Only two males exceeding 70 cm. were taken and both were mature. No female smaller than 65 cm. was mature. In the 65.0 to 69.0 cm. group about 40 per cent were mature, and above 70 cm. all were mature.

The downstream, post-spawning run began on October 8 and ended October 11. The greatest numbers of fish were caught during the hours of darkness. The fish in the run were all between 65 and 85 cm. standard length, with most of the fish over 75 cm. coming in the early part of the run. All the fish in the run were spawned out, nevertheless they were in good condition and active in the nets.

In contrast with this post-spawning run, the summer movement of inconnu from the lake to the rivers is poorly known. Most observers are in agreement that there is an early spring run of small proportions. To account for the large numbers which come down in the autumn, it would be necessary to have a more or less continuous small-scale movement all summer, or a more pronounced migration in the early autumn. Some figures from the commercial fishery in 1946 shed further light on this problem.

The weekly catch of inconnu in 1946 dropped from an average of 15,096 pounds prior to August 10 to an average of 3,861 pounds after that date. Prior to August 10, the lowest weekly total was 7,871, while between August 10 and September 15, when fishing ceased, it never rose above 5,682 pounds. The weekly catch of all other species failed to show this drop; therefore it was assumed that the declining inconnu catch represented a decrease in the availability of inconnu rather than a decrease in fishing effort.

Dr. W. A. Kennedy, Central Fisheries Research Station, has computed the catch per unit effort, which is a measure of availability, for inconnu in the commercial fishing areas of Great Slave Lake in 1946, and has kindly permitted their use here. He divided the lake into five major areas but inconnu made a significant contribution to the catch in only one area, designated "Islands". The catch per unit effort in three subdivisions of the Islands area is shown in Table IV.

The last column in this Table confirms the suggestion that there was a decrease in the availability of inconnu after August 15. A comparison of the first

TABLE IV. Catch per unit effort in the subdivisions of the "Islands" fishing area, Great Slave Lake, 1946. A unit of effort is defined as 100 yards of $5\frac{1}{2}$ -inch stretched-mesh gill net fished for one night.

	Outpost Islands	Inconnu Channel	Remainder of area
June 28-July 15	3	37	20
July 16-31	21	11	7
Aug. 1-15	34	9	2
Aug. 16-31	0.1	6	8
Sept. 1-15	...	3	4

two columns shows that as the availability decreased at Inconnu Channel it increased at Outpost Island. The most logical explanation for this observation is a mass movement in a west-southwest direction from Inconnu Channel to Outpost Island and then presumably into the open lake and eventually to the spawning streams. Dr. Kennedy informs me, however (*in litt.*), that this phenomenon has not been detected in the catch statistics for succeeding years. It is necessary, therefore, to leave the question of upstream migration in abeyance until further evidence is obtained.

FOOD HABITS

The stomachs of 196 inconnu from Great Slave Lake were examined in the field and the contents noted. The specimens in this sample varied in length from 17 cm. to 108 cm. The results of this survey indicate that the inconnu is almost exclusively piscivorous in Great Slave Lake. One hundred and eleven (57 per cent) had no food in the stomach at the time of capture; 81 fish (41 per cent) contained fish; and only 4 specimens (2 per cent) had fed on invertebrates. Although the four which had fed on invertebrates were all small fish (22 cm. to 27 cm.), there were others in the same size range, and even smaller, which had fed on fish. It is believed, therefore, that invertebrate food is the exception, rather than the rule, even for small inconnu in Great Slave Lake.

On September 1 and 2, 1946, 38 large inconnu, presumably on their way to the spawning grounds, were examined at Big Buffalo Lake. Of these, 27 had empty stomachs as might be expected. Nine others contained fish, one of them a small inconnu, while two specimens contained aquatic insects (Corixidae and Notonectidae).

Cannibalism, not observed elsewhere in Great Slave Lake under any other conditions, was recorded by Larkin (MS) at the mouth of Big Buffalo River in early October, 1945. Mature inconnu taken in the lower river before the downstream run arrived were gorged with young inconnu.

The stomachs of some of these small inconnu also yielded valuable information. Larkin found in them about 70 per cent ephippia of *Daphnia* sp., 25 per cent chironomid larvae, and 5 per cent other aquatic insects, but no amphipods or fish remains. Qualitative samples of the plankton and bottom organisms in Buffalo Lake, taken in September, 1946, showed large numbers of the cladoceran (*Daphnia pulex*), the copepod (*Epischura* sp.), ephippia of *Daphnia*, a few aquatic insects (Corixidae and Notonectidae), but no amphipods. The correlation between the food in the stomachs of the young inconnu and the food available in Buffalo Lake, and the contrast with the food of young inconnu in Great Slave Lake, suggest that these young fish were just arriving at Great Slave Lake from the upper reaches of Big Buffalo River. If this assumption is correct, then young inconnu in the rivers probably feed mainly on invertebrates and change their diet drastically on arrival at Great Slave Lake. In discussing growth rate above, it was observed that on the average there appeared to be an accelerated growth in the fourth year. These observations on the change in food habits provide a possible explanation for this accelerated growth.

In Great Slave Lake, it might appear that inconnu would compete for food with the commercially more desirable lake trout (*Cristivomer namaycush*). There are a number of reasons why competition is not considered serious. First, the two species reach their maximum abundance in different parts of the lake and do not overlap to any great extent. Trout are relatively scarce along the shallow south shore, while there are few inconnu in the deeper portions of the lake preferred by the trout. Second, there are qualitative differences in the food habits. The inconnu eats mostly small fish, up to about four inches long. It is difficult to identify these small fish because the remains are usually partially digested, but it is believed that less than 50 per cent are young ciscoes (*Leucichthys* sp.). The trout, on the other hand, subsists mainly on ciscoes which make up about two-thirds of their diet (Rawson, 1951). Third, the trout is many times as abundant as the inconnu, therefore, intraspecific competition between trout is more likely to be more severe than interspecific competition between trout and inconnu.

PARASITES

The most important parasite of the inconnu is the cestode *Triaenophorus crassus*. The larva of this worm is commonly found encysted in the flesh of whitefish and tullibee, and was therefore to be expected in inconnu, although the actual discovery, made in 1944, constituted a new host record. Because the cysts are unsightly, they render infested fish unfit for market. They do not reduce the value of inconnu as dog feed because *Triaenophorus* is not pathogenic in mammals.

Examination of the larval cysts was made by filleting the fish and cutting transverse sections of the fillets about one-eighth of an inch thick. The results of a series of examinations made in 1945 and 1946 are shown in Table V. The degree of infestation is high for all the subsamples, which are taken from several localities in the lake, and at various times throughout the season. The reasons for this high rate are obvious. Pike (*Esox lucius*) are the adult hosts of *Triaenophorus*, and they are abundant in the Big Buffalo River and the other spawning

TABLE V. *Triaenophorus* infestation of Great Slave Lake inconnu.

Date and place	Fish examined		Fish infested		Degree of infestation	
	Number	Weight lb.	Number	Per- centage %	Total cysts	Cysts per 100 lb.
Resolution, June 23/45	1	10.5	1	100	7	67
Outpost Island, June 25/45	3	21.8	2	67	13	60
Outpost Island, June 30/45	2	12.0	2	100	7	58
Gros Cap, Aug. 2/45	5	45.0	3	60	24	53
Gros Cap, Aug. 5/45	5	48.5	4	80	23	47
Big Buffalo River, June 24/46	5	37.5	4	80	18	48
Big Buffalo River, June 25/46	14	67.0	14	100	88	132
Big Buffalo Lake, Sept. 1/46	8	87.0	7	88	31	36
Big Buffalo Lake, Sept. 2/46	6	46.5	6	100	29	62
TOTAL	49	375.8	43	88	240	64.0

streams of the inconnu. The first larval stage of *Trienophorus* is spent in the copepod *Cyclops*, and it has been shown that young inconnu feed to a large extent on copepods.

Other parasites recovered from inconnu were submitted to Dr. R. B. Miller, University of Alberta, for identification. Dr. Miller has kindly supplied the following list:

Proteocephalus sp. nov.—Intestine

Eubothrium sp.—Intestine

Salmincola (probably new species)—Gills

ECONOMIC IMPORTANCE AND MANAGEMENT

THE COMMERCIAL FISHERY

When McInnes Products Corporation initiated commercial fishing operations in Great Slave Lake in 1945, the inconnu formed a significant part of the catch of the fishermen. The company therefore bought inconnu and sought to develop a market. In this they were not successful. Most local residents do not like fresh inconnu, although the writer, other members of the field party and a group of fisheries experts assembled in conference in Edmonton all found it quite palatable. The inconnu also has a high fat content which reduces its keeping qualities and therefore detracts from its value on distant markets, at least in the fresh or frozen states.

The writer has eaten inconnu smoked by the late W. Greer, who formerly lived at the mouth of the Big Buffalo River. This product was excellent and somewhat suggestive of smoked goldeye (*Amphiodon alosoides*). Smoking might provide an answer to the marketing problem.

The amount of the catch in 1946 was 130,000 pounds, or about 5 per cent of the commercial catch of all species from Great Slave Lake.

THE DOMESTIC FISHERY

The most important local use of the inconnu is for dog feed. It is favoured by the trappers because, being a shallow-water fish, it is easily taken all summer, and because large numbers may be easily caught during the fall run and hung to dry for winter use. The amount of the catch at Big Buffalo River has been estimated to be as high as 100,000 pounds annually. When the fall catches at Taltson and Hay Rivers and Fort Smith and the summer fisheries around the lake are added to this, a conservative estimate of the total annual domestic consumption would probably be about 150,000 pounds.

MANAGEMENT IMPLICATIONS

A random sample of 342 inconnu from the commercial catch was measured on July 4 and 5, 1946. In this sample approximately 8 per cent were immature; 51.5 per cent were in the size range 55.0 to 69.5 cm. (i.e. fish maturing in the present season or fish which had spawned only once); and 54 per cent were in the range 65.0 to 74.5 cm. (i.e. the size which made up the major portion of the spawning run in 1945). It is apparent that the commercial gear (5½-inch mesh

gill nets) is taking a high proportion of non-spawners, and fish which have probably only spawned once.

The domestic fishery also depends heavily on fish in the early reproductive years, and the practice of using nets to block spawning streams completely is probably not in the best interest of conservation. This practice apparently had no harmful effects on the inconnu population from early times until commercial operations began in 1945. With the advent of a commercial fishery, however, the overall rate of exploitation has approximately doubled. This creates a situation which should be watched in the future in order to safeguard a supply of inconnu for local needs.

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Food and Feeding Habits of Brünnich's Murre (*Uria lomvia lomvia*) on Akpatok Island¹

BY LESLIE M. TUCK² AND H. J. SQUIRES³

ABSTRACT

A study of the food and feeding habits of Brünnich's murre (*Uria lomvia lomvia*) on Akpatok Island, Ungava Bay, was made during the period August 9-28, 1954. The adults often dropped the food they were bringing to the young. This was collected in a restricted area, daily. Some young were fed experimentally with this food which showed that 13.4 grams were required to build a gain in weight of 1 gram.

Examination of the stomach contents of 34 adults showed a predominance of crustaceans but the presence of otoliths and vertebrae suggest that fish are a large part of the diet of the adult as well. Twenty species of fish and 12 of invertebrates are identified and discussed with relation to their occurrence in the area and proportion in the food of the young murre.

A first record for the Eastern Canadian Arctic, *Onchidiopsis glacialis* (M. Sars), is recorded.

INTRODUCTION

THE SENIOR AUTHOR accompanied by Mr. John B. Millar⁴ spent from July 10 to August 29, 1954, on Akpatok Island in Ungava Bay undertaking a study of two large colonies of Brünnich's murres (*Uria lomvia lomvia*) which occupy the island during the summer months. The Brünnich's murre is a member of the Alcidae and with its Pacific counterpart is circumpolar in distribution. In North America it breeds rarely south of 60°N. latitude. It winters to a great extent in the offshore zone around Newfoundland. Normally, it does not approach land except during the breeding season when it nests in large colonies on steep cliffs facing the sea.

A section of the southern colony under study was subjected to gravity winds. Consequently, the adult murres bringing food to the young often found themselves in difficulties when landing on the narrow ledges. Quite frequently they dropped food which fell on the scree at the base of the cliff. A daily collection of this food was made, commencing at the peak of the hatch, in a restricted area approximately one mile long and six feet wide. The results indicated that this system of collecting was fairly consistent, as daily percentages were approximately constant throughout the period of collecting.

The breeding period of this species on Akpatok Island is much compressed and the greater number of eggs were laid during a few days in early July. Consequently, the peak hatching period occurred during the first week in August. The young murres fledged, or left the colony of their own accord, between 23

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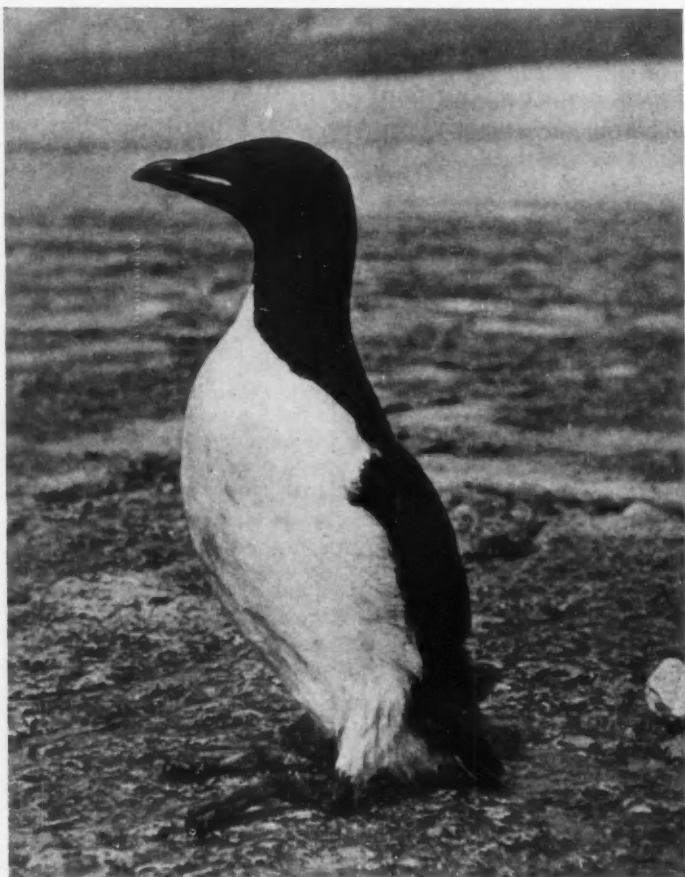


FIGURE 1. Adult Brünnich's murre, Akpatok Island, 1954.

and 24 days of age. Our collection, then, was begun on August 9 and terminated on August 29 in order to coincide with the feeding of the greatest number of young birds by the adults. The first fledgling had left the colony on August 26.

Ten young murres were captured when they were approximately six days of age. They were kept and fed on some of the dropped food which the adults were bringing to the colony. One was fed exclusively on amphipods collected from tide-pools along the sea-shore.

The object of this paper is to discuss the feeding relationships of the Brünnich's murre and the species of fish and invertebrates which are predominant in its collected food. The adults foraged presumably at random in an area near the colony. Therefore, the food species in the collection may be regarded as repre-

sentative of this region. Notes are made on individual species because collections of fish and invertebrates which may be considered sedentary in this region are comparatively rare.

FEEDING HABITS OF THE MURRE

The Brünnich's murre obtains its food from the sea by diving and it has been occasionally caught off Newfoundland on longline trawls set at 40 fathoms or more. The murre's short wings are well adapted for use under water. It can pursue its prey by a method of subaqueous flight which has also been developed

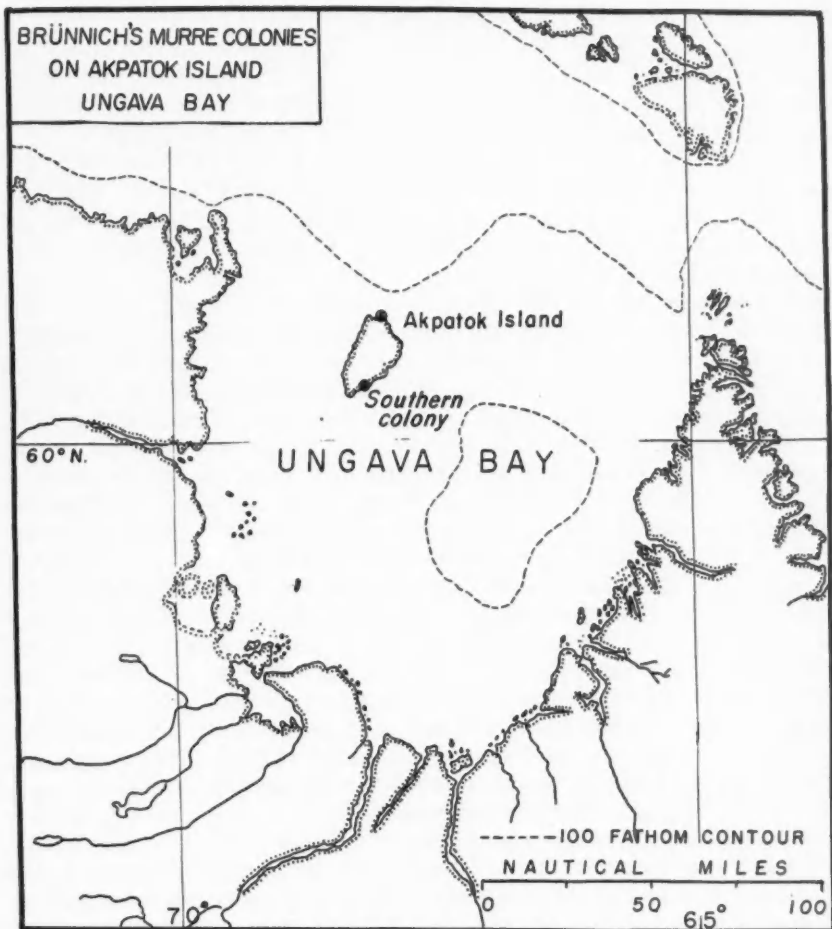


FIGURE 2. Location of Brünnich's murre colonies, Akpatok Island.

by the penguins of the southern hemisphere, a supposedly unrelated group. No actual data on depth of feeding off Akpatok Island could be obtained, but bottom depths in this area range to about 60 fathoms. The fish and invertebrates taken by the murres in this area were mostly bottom-dwelling forms so that the birds had to dive to a considerable depth to feed.

Early in the nesting period the adults foraged in large groups. As incubation progressed, and particularly after the young had hatched, the birds were observed most frequently to forage singly. Both sexes participated in bringing food to the young and individual parents were absent from the colony for about one hour on each foraging expedition; the young one rarely being left unattended.

The birds foraged in an area not greater than ten miles in radius from the colony with the greatest concentrations from one to five miles offshore. Thus the two colonies, some thirty miles apart, were separated by a ten-mile stretch of coastal water in which murres were virtually absent. The same situation existed offshore; the presence of murre colonies in the vicinity remained completely undetected until the boat (or aircraft) came within ten miles of the colonies.

Winds did not seem to influence their choice of feeding areas—which appeared to be at random within this zone—but they did influence the approach of the birds to the 800-ft. vertical cliffs on which they nested. Consequently, on stormy days, the birds fed infrequently, and on a particularly stormy day such as August 24, they did not leave the colony at all.

The adult birds occasionally brought fish to the nesting sites a week or so before the young were hatched. On these occasions the adult was not observed to feed its incubating mate but would remain nearby for long periods merely holding the fish in its bill. The eggs began to hatch during the first week in August and immediately the tenor of the colony changed. When previously the colony was comparatively quiet during the darkest hours of the night, now there was continuous clamour. Now also, soon after sunrise and all through the daylight hours, unless the day were stormy, the adults were in continuous flight to and from the sea. On these return flights, they invariably returned with fish. Only rarely did the birds bring more than one fish at a time and occasionally a fish was held crosswise. Normally, the fish was held lengthwise with the tail overhanging the bird's bill and the head usually well down in the gullet. The adults before presenting the fish to the young went through lengthy ceremonies involving complex motions of the head and frequent bowing. Before being presented to the young, the fish were retained by the adult for a considerable amount of time as a rule, sometimes as long as one hour. This may be biologically important as the tough heads of such species as the mailed sculpin were found to be softened or partially digested. After the ceremonies, the adults presented the food directly to the young or laid it nearby.

In the feeding experiments, the young were fed immediately after capture. At first fish were dangled in front of them. Later, the food was dropped on the ground and they fed themselves. Fish up to 15 cm. in length were eagerly taken by young scarcely one week old. They went through prolonged contortions while swallowing. If the fish were particularly large they remained inert with eyes

closed as the fish was being digested while ripples of muscular reaction passed over their bodies. The young murrens sometimes had difficulties with the tough heads of the mailed sculpins and we sometimes rescued a bird from what we considered certain strangling. There was no evidence, however, that mortality from strangling occurred on the nesting ledges. This was because the heads of these fish were softened beforehand by the adults as mentioned above.

FOOD OF ADULT MURRENS

The contents of 34 stomachs of adult Brünnich's murrens were preserved. Approximately 85% of the total amount of food consisted of amphipods. Almost all amphipods found were Hyperids but a few fragments of Gammarids were present. A few fish vertebrae, and many otoliths from Atlantic cod, Arctic cod, *Lycodes* sp., *Lumpenus* sp., *Liparis* sp. and mailed sculpin were present. In addition, there were many jaws of polychaete worms and a few pebbles.

Undoubtedly, fish are digested in a murre's stomach much faster than chitinous amphipods and this would account for the disproportionately small quantity of fish remains as compared with remains of amphipods.

FOOD OF YOUNG MURRENS

There was, evidently, a very high incidence of fish (93.7%) in the diet of the young murrens (Table I). On the basis of volume of specimens dropped by the adults, fish formed at least 99% of the total food because the combined weight of the 172 invertebrates in the sample collected was approximately equal to the weight of only three or four of the larger fish.

It is quite possible that some of the small invertebrates which were dropped were overlooked in the loose scree on which we collected. It is also possible that these small organisms were dropped less frequently than the relatively larger fish.

Of the fishes, the greatest numbers taken were Arctic cod (34.5%), mailed sculpin (26.7%) and blennies (19.8%). Together these comprised 81% of the total numbers and an even greater part of the volume because these species were the largest utilized by the murrens. For instance, the majority of the Arctic cod and mailed sculpin weighed on the average about 25 grams each, while the combined weight of the 118 Greenland halibut in the collection was approximately 150 grams. The blennies were comparable in weight as well as number with Arctic cod and mailed sculpin. The unidentified fish remains were those so badly damaged that key characters were missing. For example, the lantern fish were damaged and had lost most of their scales.

Among the invertebrates, the Arctic squid was predominant but, except for one individual, all were quite small. The most frequently found species of shrimp was *Argis dentata*.

It appears that the most important foods of the young Brünnich's murre in Ungava Bay are Arctic cod, mailed sculpin and blennies which are Arctic and sub-Arctic forms, and that other fish species and invertebrates are taken in-

cidentally. Capelin, which figures largely in the diet of the species on its wintering grounds off Newfoundland, was of low incidence, possibly because there were so few in the area.

TABLE I. Percentages of fishes and invertebrates in sample of Brünnich's murre food to young, August 9-28, 1954. Akpatok Island.

Species	English name	Number of individuals	Percentage of total
FISHES			
<i>Mallotus villosus</i> O. F. Müller	Capelin	38	1.40
Myctophidae	Lantern fish	2	0.07
<i>Boreogadus</i> sp.	Arctic cod	931	34.50
<i>Eumesogrammus praecisus</i> (Krøyer)	Blennies	536	19.84
<i>Lumpenus lumpretaeformis</i> (Walbaum)			
<i>Lumpenus maculatus</i> (Fries)			
<i>Lumpenus facricii</i> Reinhardt			
<i>Lumpenus medius</i> Reinhardt			
<i>Gymnelis viridis</i> (Fabricius)			
<i>Gymnelis stigma</i> Fay & Bennett	Launce	36	1.33
<i>Ammodytes americanus</i> De Kay			
<i>Sebastes marinus</i> Linné	Redfish	1	0.04
<i>Icelus bicornis</i> Reinhardt	Two-pronged sculpin	4	0.15
<i>Triglops pingeli</i> Reinhardt	Mailed sculpin	721	26.69
<i>Myoxocephalus scorpioides</i> (Fabricius)	Arctic sculpin	2	0.07
<i>Gymnocanthus tricuspis</i> (Reinhardt)	Stag-horn sculpin	1	0.04
<i>Eumicrotremus spinosus</i> (Müller)	Spiny lumpfish	24	0.89
<i>Liparis tunicatus</i> Reinhardt	"Sea-snails"	45	1.66
<i>Liparis koefoedi</i> Parr			
<i>Reinhardtius hippoglossoides</i> (Walbaum)	Greenland halibut	118	6.67
Unidentified fish remains	...	9	0.33
Total fish:		2,530	93.70
ANNELIDA			
<i>Eunoë nodosa</i> (Sars)	...	1	0.04
<i>Nereis</i> sp.	Sand-worm	2	0.07
AMPHIPODA			
<i>Gammarus</i> sp.	...	1	0.04
<i>Gammarus wilkitzkii</i> (Birula)	...	1	0.04
<i>Anonyx nugax</i> Krøyer	...	2	0.07
DECAPODA			
<i>Pandalus montagui</i> Leach	Shrimp	7	0.26
<i>Lebbeus polaris</i> (Sabine)			
<i>Lebbeus groenlandicus</i> (J. C. Fabricius)	...	32	1.19
<i>Spirontocaris spinus</i> Sowerby			
<i>Argis dentata</i> Rathbun	...	55	2.04
MOLLUSCA			
<i>Gonatus fabricii</i> Verrill	Arctic squid	70	2.59
<i>Onchidiopsis glacialis</i> (M. Sars)	...	1	0.04
Total invertebrates:		172	6.30

EXPERIMENTAL FOOD UTILIZATION

Our first experiment was started on August 7 when we commenced to feed a nestling about four days of age and weighing 60 grams with the amphipod *Gammarus* sp. collected from tide-pools along the seashore. On the subsequent three days, it ate 127, 200 and 190, respectively, of these amphipods. At first it flapped its wings, preened after each feeding and appeared quite active. On

August 11, it no longer ate eagerly and gradually became sluggish and died. During the experiment it gradually lost weight and at its death weighed 50 grams. We had noted that its excrement had become progressively solid and was composed mainly of undigested chitin.

Ten nestlings in all were used in another experiment (Tables II, III). Two of these were eventually found to be injured and were destroyed. The food consisted principally of Arctic cod and mailed sculpin with an occasional offering of Greenland halibut and capelin. The young were weighed each morning before feeding and were fed twice each day.

The nestlings usually lost weight for the first day or two (Table II). This could probably be attributed to either shock or a change in the environment. On a few of the days, they either made no gain or lost slightly and this was un-

TABLE II. Daily individual weights (in grams) of experimentally fed young Brünnich's murres, Akpatok Island. (Birds No. 2 and 5 were found to be injured and were destroyed. All others were banded on date last recorded and released.)

August	No. 1	No. 2	No. 3	No. 4	No. 5	No. 6	No. 7	No. 8	No. 9	No. 10
14	160									
15	140	125	165							
16	140	110	150	100	90	125				
17	140	90	150	100	75	125	75	130		
18	150		150	110	75	110	80	110	150	100
19	175		175	130	90	115	100	135	130	100
20	175		175	130	70	125	90	140	150	110
21	175		180	140	90	125	110	150	140	120
22	200		210	150	90		125			
23	200		215	150	100		130			
24	225		220	170	100		160			
25	225		225	175			170			
26	230		220	170			175			
27	235		220	160			165			
28	250		230	175			175			
29	260		225	160			170			

TABLE III. Experimental food utilization (in grams) of young Brünnich's murres, Akpatok Island.

Date, August	Number of birds	Total weight at beginning of period	Total food consumed	Total weight at conclusion of period	Net change
		g.	g.	g.	g.
16	6	715	290	680	-35
17	6	665 ^a	325	655	-10
18	9	1,035	775	1,130	95
19	9	1,130	530	1,165	35
20	9	1,165	710	1,230	60
21	5	695	590	775	80
22	5	775	490	795	20
23	5	795	600	875	80
24	4	775	500	795	20
25	4	795	410 ^b	795	0
26	4	795	335 ^b	780	-15
27	4	780	525	830	50
28	4	830	425	815	15

^aOne bird died and was replaced by a younger individual.

^bFull requirements of food not given on these days.

doubtedly due to our not being able to satisfy their requirements from our daily collections of food. During this period we used four of the experimentally fed birds for another experiment involving adult-recognition. The remaining four, which were kept until August 29, compared very favourably in weight with nestlings of similar ages which had been fed by the adults on the nesting ledges.

Table III indicates that 6,505 grams of food are required to build a body weight of 395 grams. However, if the first two days are eliminated from the calculations to make an adjustment for the unnatural loss of weight due to shock, 5,890 grams of food are required to build a weight of 440 grams, or 13.4 grams of food per gram gained. Thus the young murre requires approximately half of its weight in food daily. The young were fledged, and left the colony, at between 23 and 24 days of age weighing between 250 and 275 grams.

GROSS UTILIZATION OF FISH BY MURRES

The estimated population of the two large colonies of Brünnich's murres on Akpatok Island was 1,200,000 birds. The breeding potential is low because the species is able to brood only a single egg. The productivity is also low because eggs and young are frequently knocked off the narrow ledges. It was estimated that the increment for 1954 was approximately 25% or 300,000 young successfully fledged. By the end of August, these birds would be utilizing 50 tons of food daily. There are no data available for the actual amount of food consumed by the adults, but assuming they feed regularly during this period and that the amount is one half-pound per day per bird, the adults in the colonies would consume an additional 300 tons daily. These estimates give some idea of the productivity of the waters surrounding Akpatok Island particularly with reference to fish, most of which, however, are not considered to be commercial species.

DAILY OCCURRENCE OF PRINCIPAL FOOD BROUGHT TO YOUNG

A further consideration of the occurrence of species in the sample is shown in Table IV, which is a record of the daily collections of predominant species. It will be seen that Arctic cod had a high incidence on the first few days and decreased in numbers towards the end of the period, while the mailed sculpin showed a low incidence at the beginning of the period and increased in numbers towards the end. The number of blennies remained fairly constant and this is also true of other species. The Arctic squid fluctuated more than other species but this may be due to their variable habits of schooling. Generally, it may be observed that a high incidence of mailed sculpins was accompanied by a low incidence of blennies, so it would appear that blennies were selected against. Since blennies are probably easily obtained and since they are comparatively bulky, they may be taken to provide bulk when mailed sculpins are not available. On the other hand, the majority of the mailed sculpins were gravid and may have been selected because they were sluggish and easily caught, rather than because they were preferred.

TABLE IV. Daily occurrences (in percentages) of principal fishes and invertebrates in Brünnich's murre food to young August 9-28, 1954, Akpatok Island.

Date	<i>Mallotus</i>	<i>Boreogadus</i>	Blennies	<i>Ammodytes</i>	<i>Triglops</i>	<i>Reinhardtius</i>	<i>Argis</i>	<i>Gonatus</i>	Others
Aug. 9	...	53.8	20.5	...	10.3	5.1	2.6	7.7	...
Aug. 10	...	46.3	25.4	...	23.9	1.5	2.9
Aug. 11	1.6	40.4	24.2	1.6	17.8	6.5	...	3.2	4.7
Aug. 12	0.8	46.5	18.1	...	18.1	3.9	2.4	4.7	5.5
Aug. 13	...	42.2	13.2	...	23.7	13.2	5.3	...	2.4
Aug. 14	4.8	30.2	25.6	1.2	24.4	6.6	1.2	1.8	4.2
Aug. 15	...	29.5	20.5	1.0	30.5	7.2	1.9	3.3	6.1
Aug. 16	0.4	42.3	17.8	1.6	26.4	4.7	0.8	2.3	3.7
Aug. 17	1.2	36.1	12.7	0.3	26.8	4.6	2.5	1.5	14.3
Aug. 18	3.0	26.1	15.3	0.5	32.5	7.9	3.9	2.0	8.8
Aug. 19	2.3	30.9	22.1	0.9	29.5	3.7	3.7	2.3	4.6
Aug. 20	0.6	32.1	22.4	3.2	22.4	10.9	1.9	0.6	5.9
Aug. 21	2.9	30.3	13.6	...	32.0	7.8	2.0	2.0	9.4
Aug. 22	...	34.2	15.3	0.6	24.2	8.9	1.9	8.9	6.0
Aug. 23	3.0	30.8	18.8	3.0	24.1	9.8	1.5	2.3	6.7
Aug. 24	Birds not fishing—very stormy					
Aug. 25	1.4	32.7	20.6	3.7	23.4	8.0	2.3	3.7	4.2
Aug. 26	...	33.3	16.3	2.3	30.2	8.5	1.6	...	7.8
Aug. 27	3.1	28.1	3.1	3.1	53.2	6.3	3.1
Aug. 28	...	30.8	16.9	3.1	37.0	7.7	4.5

NOTES ON FISHES LISTED IN TABLE V

CAPELIN, *Mallotus villosus* O. F. Müller

According to the method of reading the ages from scales (Templeman, 1948) none of these were more than two years of age. Their daily occurrence (Table IV) showed that schools were nearby during most of August.

ARCTIC COD, *Boreogadus* sp.

These Arctic cod were distinct from *Boreogadus saida* Lepechin which are common in cold water areas in Newfoundland. Since the work of the Russian authors referred to by Dunbar and Hildebrand, 1952, is not available to us at present, the taxonomy of this species is deferred.

BLHENNY, *Lumpenus maculatus* (Fries)

Unlike the findings of Dunbar and Hildebrand, the present collection shows this to be the most abundant of the genus in Ungava Bay. Since their collections were made from the stomach contents of Atlantic cod, a difference in the feeding habits of cod and Brünnich's murre is probably indicated. When the pectoral rays are damaged, it is possible to identify this blenny by colour and the conspicuous gap between the dorsal and caudal fins (Jensen, 1944). This gap is absent in *L. medius* and almost completely occupied by a membrane in *L. fabricii*. From coloration and the presence of a gap between the dorsal and caudal fins the two post-larval specimens of *Lumpenus* were most probably *maculatus*.

***Gymnelis viridis* (Fabricius), and *Gymnelis stigma* Fay & Bennett**

These do not appear to be distinct from each other except in the possession of dark ocellated spots by *G. stigma* (Jordan and Everman, 1898). The spots are

TABLE V. Meristic characters of fishes in Brünnich's murre food to young August 9-28, 1954, Akaptok Island.

Species of fish	Number examined	Length range	Average length	Fin ray counts—range			
				Dorsal	Pectoral	Anal	Ventral
<i>Mallotus villosus</i>	11	cm. 9.5-12.0 (6)	cm. 10.8 (6)				
<i>Boreogadus</i> sp. (not <i>saida</i> of Lepechin)	5	8.4-13.2 (3)	11.4 (3)	9-12, 14-16, 20-21 (4) (4) (4)	18, 19 (3)	20 (4)	6 (3)
<i>Eumesogrammus praecisus</i>	6	8.1-14.9 (6)	10.5 (6)	XLVII-L (Av. XLIX) (6)	17, 18 (6)	31-35 (6)	
<i>Lumpenus lumpretaeformis</i>	3	17.5-21.0 (3)	19.4 (3)	74-77 (Av. 75) (3)	15, 16 (2)	51-52 (2)	
<i>Lumpenus maculatus</i>	17	9.3-15.5 (10)	11.5 (10)	59-62 (Av. 60) (7)	14-16 (10)	33-36 (4)	
<i>Lumpenus fabricii</i>	1	17.8		63	15	42	
<i>Lumpenus medius</i>	1	12.3		60	14	41	
<i>Lumpenus</i> sp. (young <i>maculatus</i> ?)	2	6.8- 7.1 (2)	7.0 (2)	53 (2)	14, 15 (2)	37 (2)	
<i>Gymnelis viridis</i>	12	9.5-16.8 (12)	12.5 (12)	83-93 (Av. 89) (4)	13-15 (10)	65-74 (4)	
<i>Gymnelis stigma</i>	9	10.1-17.0 (9)	14.0 (9)	85-93 (Av. 89) (3)	12-14 (5)	73-76 (3)	
<i>Ammodytes americanus</i>	25	5.8-10.8 (23)	8.2 (23)	59-68 (Av. 63) (22)	11-14 (20)	27-35 (22)	
<i>Sebastes marinus</i>	1	5.7		XV, 13	18		
<i>Icelus bicornis</i>	4	6.7- 8.6 (3)	7.7 (3)	VIII-IX, 19-21 (4)	17-19 (4)	14-16 (4)	
<i>Triglops pingeli</i>	3	6.1-14.6 (3)		XXI, 25, 26 (3)	17-21 (3)	23-26 (3)	
<i>Myoxocephalus scorpioides</i>	2	6.5-10.0 (2)	8.3 (2)	X, 15, 17 (2)	17 (2)	12, 13 (2)	
<i>Gymnocanthus tricuspis</i>	1	5.6		XI, 16	18	17	
<i>Eumicrotremus spinosus</i>	7	4.4-7.5 (7)	5.4 (4)	6-8, 9-12 (4) (4)	23-26 (6)	10, 11 (6)	
<i>Eumicrotremus spinosus variabilis</i> Jensen	11	4.1-6.8 (11)	4.9 (11)	7, 8 11, 12 (3) (8)	25-27 (7)	9-12 (8)	
<i>Liparis tunicatus</i>	4	6.0-9.6 (3)	8.2 (3)	42-44 (Av. 43) (4)	35-40 (4)	32-36 (4)	
<i>Liparis koefoedi</i>	12	5.6 (3)	5 (3)	41-49 (Av. 46) (6)	36-38 (3)	32-44 (7)	
<i>Reinhardtius hippoglossoides</i>	4	9.0-14.0 (4)	10.8 (4)	99 (1)		68 (1)	

large, close to the dorsal fins and always in pairs. In the nine specimens examined, seven had one pair of spots, one had three pairs and one had four pairs.

LAUNCE. *Ammodytes americanus* De Kay

This naming is used for the specimens from Akpatok Island. However, the fin ray counts of these would refer it to *A. dubius* Reinhardt, but larger specimens from Newfoundland have a similar fin ray count and are in the geographical range of *A. americanus*. A few specimens from Labrador of the same size as those from Akpatok Island have fin ray counts of *A. americanus* De Kay. The two names are probably synonymous (Bigelow and Schroeder, 1952).

REDFISH. *Sebastes marinus* Linné

There was apparently one annulus on the scales of this specimen so the fish was probably a two-year-old (Perlmutter and Clarke, 1947).

MAILED SCULPIN. *Triglops pingeli* Reinhardt

This species would appear to be equivalent to *Triglops ommatistius* Gilbert, in that the colour pattern and meristic characters of *pingeli* are very variable showing an overlap with those of *ommatistius* as described by Gilbert (Jensen, 1944); but the central ray in the ventral fin is always the longest in males, and the innermost ray of the ventral fin is always the longest in females (W. Templeman, pers. comm.). However, this was one of the characters used by Jensen (1944) to erect a new species *nybelini*. The fin ray counts of the specimens from Akpatok Island all but overlap the counts for *nybelini* (Table V) yet they are otherwise typically *pingeli*.

SEA-SNAIL. *Liparis koefoedi* Parr

Two of these were parasitized by *Haemobaphes cycloptera* (Fabricius), (Copepoda, Lernaedidae), which had head processes inserted in the branchial arches and were almost concealed by the gill-covers.

SPINY LUMFFISH. *Eumicrotremus spinosus* (Müller)

Our specimens belong undoubtedly to this species but a few have spiny tubercles on the chin, a character which has been used to distinguish another species *E. terra-novae* (Myers and Böhlke, 1950). However, the spiny tubercles seem quite variable in number and position in this species and the names may be synonymous.

Eumicrotremus spinosus variabilis Jensen

Our specimens were quite dark, with few to many spiny tubercles, some of which covered the enclosed first dorsal fin. The first dorsal fin is farther posterior and the anus is much farther from the smaller disc than in *spinosus*. The fin rays appear to have a higher count also (Table V). There are no tubercles with spines anterior to the anus ventrally in *E. s. variabilis*.

NOTES ON INVERTEBRATES LISTED IN TABLE I.

ARCTIC SQUID. *Gonatus fabricii* Verrill

The largest of those examined had a mantle length of 8 cm. The mantle lengths of the others averaged less than 4 cm.

Onchidiopsis glacialis (M. Sars)

The osphradium of this specimen was colourless, unlike the black-based osphradium of other species of the genera listed by Balch, 1910. The internal shell was corneous and transparent. It is referred, therefore, to the species, *glacialis*. Thorson, 1941, lists *O. groenlandica* for Iceland and West Greenland but it is not certain that his species is synonymous with *O. glacialis* which is listed for East Greenland only. This, we believe, is a first record for the Ungava Bay area and perhaps for the Eastern Canadian Arctic.

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